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FINAL REPORT

TEMPORAL AND SPATIAL VARIATION IN THE DEMOGRAPHIC RATES OF TWO MEXICAN SPOTTED OWL POPULATIONS

PRINCIPAL INVESTIGATOR

R. J. GUTIÉRREZ
UNIVERSITY OF MINNESOTA

PROJECT LEADERS

CHRISTOPHER A. MAY
MYLEA L. PETERSBURG

RESEARCH COLLABORATOR

MARK E. SEAMANS

CONTRACTING AGENCY

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Christopher A. May
Department of Fisheries, Wildlife, and Conservation Biology
University of Minnesota
St. Paul, MN 55108

601-268-0461; Email chrismay@merlin.ebicom.net

TEMPORAL AND SPATIAL VARIATION IN THE DEMOGRAPHIC RATES OF TWO MEXICAN SPOTTED OWL POPULATIONS

CHRISTOPHER A. MAY[1]

Department of Fisheries, Wildlife, and Conservation Biology, University of Minnesota, St. Paul, MN 55108, USA.

MYLEA L. PETERSBURG[2]

Department of Fisheries, Wildlife, and Conservation Biology, University of Minnesota, St. Paul, MN 55108, USA.

R. J. GUTIÉRREZ

Department of Fisheries, Wildlife, and Conservation Biology, University of Minnesota, St. Paul, MN 55108, USA.

MARK E. SEAMANS

Department of Fisheries, Wildlife, and Conservation Biology, University of Minnesota, St. Paul, MN 55108, USA.

Abstract: We studied Mexican spotted owl (*Strix occidentalis lucida*) population dynamics on 1 study area in Arizona (n = 63 territories) and 1 study area in New Mexico (n = 47

territories) from 1991-2002. We estimated the degree to which climate and habitat covariates explained temporal and spatial variation, respectively, in population parameters. In addition, we estimated the population rate of change for owls on each study area. Mean annual apparent survival was 0.859 (SE = 0.041) and 0.856 (SE = 0.022) in Arizona and New Mexico, respectively. Mean annual reproductive output (the number of young fledged per territorial pair) was 0.929 (SE = 0.188) and 0.702 (SE = 0.199) in Arizona and New Mexico, respectively. Within each study area, reproduction varied greatly over time, while survival varied little. The amount of temporal variation explained by climate varied by population parameter and study area. With the exception of survival in New Mexico, more days with measurable precipitation during important periods of the spotted owl annual cycle positively affected survival, reproductive output, and recruitment on both study areas. In New Mexico, the most parsimonious climate model, which included monsoon precipitation, explained none of the temporal process variation in owl survival; sampling error accounted for most (60%) of the variation in this parameter. Annual precipitation explained only 12% of the variation in reproductive output in New Mexico. In Arizona, a moisture index (Palmer Z Index) explained 52% and 42% of the temporal process variation in owl survival and reproductive output, respectively. Habitat covariates explained little of the estimated spatial process variation in survival on either study area and reproduction in New Mexico. The area (ha) of mature forest in owl territories accounted for 8% of the spatial process variation in owl survival in Arizona, although the relationship was unclear based on the confidence interval. The area (ha) of pine and pine-oak forest (all seral stages

combined) accounted for 100% of the spatial process variation in reproductive output (positive relationship) in Arizona; however, most (92%) of the variation in this parameter was due to sampling error, which left little process variation to be explained by the habitat covariate. Approximately 27% of the spatial process variation in survival of owls in New Mexico was explained by an additive combination of the length of edge between spotted owl habitat and other habitats, the maximum patch size of spotted owl habitat, and the total area of core spotted owl habitat. The amount of "other" habitat (defined as habitat not used for nesting or roosting by spotted owls) in territories accounted for 4% of the spatial process variation in owl reproductive output (negative relationship; confidence interval included zero) in New Mexico. We estimated mean annual recruitment rates of 0.145 (SE = 0.041) and 0.089 (SE = 0.035) for Arizona and New Mexico, respectively. A moisture index (Palmer Z Index) explained 32% and 84% of the temporal process variation in owl recruitment in Arizona and New Mexico, respectively. Estimates of the population rate of change (λ) indicated that the Arizona population was stable (mean λ from 1993 to 2000 = 0.995; 95% CI = 0.836, 1.155) over the course of study while the New Mexico population declined at an annual rate of about 6% (mean λ from 1993 to 2000 = 0.937; 95% CI = 0.895, 0.979). We used a model validation procedure to estimate, *a priori*, 2002 reproductive output on both study areas. Estimates from this validation procedure differed from empirical estimates of 2002 reproductive output by 12% and 14% in Arizona and New Mexico, respectively.

Our results were different than those reported for northern spotted owls (*S. o. caurina*)

and Mexican spotted owls. Some of these differences may be the result of greater variation in climate and habitat associated with our study populations and study areas.

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Keywords: Arizona, climate, habitat, mark-recapture, Mexican spotted owl, model selection, New Mexico, population dynamics, population rate of change, process variation, recruitment, reproduction, *Strix occidentalis lucida*, survival

Contents

INTRODUCTION

Acknowledgments

METHODS

Study Areas

Field Effort

Surveys and monitoring

Biological Hypotheses, Predictions, and *A Priori* Model Development

Biological basis for delineating important time periods of the spotted owl annual cycle

Climate model development

Habitat model development

Covariate Estimation

Climate covariates

Habitat covariates

Data Analysis

Survival

Reproductive output

Model validation using 2002 reproductive output

Recruitment

Components of variation

Population rate of change

RESULTS

Population Dynamics of Spotted Owls in Arizona

Field effort in Arizona

Effects of climate on owl survival in Arizona

Effects of climate on owl reproduction in Arizona

Model validation using 2002 reproductive output in Arizona

Effects of climate on owl recruitment in Arizona

Population rate of change in Arizona

Effects of habitat on owl survival in Arizona

Effects of habitat on owl reproductive output in Arizona

Population Dynamics of Spotted Owls in New Mexico

Field effort in New Mexico

Effects of climate on owl survival in New Mexico

Effects of climate on owl reproductive output in New Mexico

Model validation using 2002 reproductive output in New Mexico

Effects of climate on owl recruitment in New Mexico

Population rate of change

Effects of habitat on owl survival in New Mexico

Effects of habitat on owl reproductive output in New Mexico

DISCUSSION

Climate and Temporal Variation in Population Parameters

Survival

Reproductive output

Recruitment

Habitat and Spatial Variation in Population Parameters

Population Rate of Change and Relationships Among Estimated Population Parameters

Management Implications

LITERATURE CITED

INTRODUCTION

The Mexican spotted owl has the largest geographic distribution of the 3 recognized spotted owl subspecies (Gutiérrez et al. 1995). Across this extensive range, the owl occupies many habitats, ranging from steep-sided canyons with few trees to extensive stands of mixed conifer forest (Gutiérrez et al. 1995, Ward et al. 1995). It is found as large,

contiguous populations and as small isolated populations. In addition, it is geographically isolated from northern and California spotted owls (*S. o. caurina* and S. *o. occidentalis*, respectively) and is genetically distinct from the coastal spotted owl subspecies, indicating that the Mexican spotted owl is evolving independently of the other subspecies (Barrowclough et al. 1999).

The diverse habitats used by the owl and the varying sizes of many, separate populations present unique challenges for Mexican spotted owl management. Many of the areas it inhabits are relatively remote, which has inhibited its ecological study, especially in Mexico where its range spans more than 2,400 km from north to south. Thus, relatively little is known about the Mexican spotted owl's population ecology (Seamans et al. 1999). Concern over the conservation status of the northern and California spotted owls (Thomas et al. 1990; Verner et al. 1992) has stimulated research not only on these subspecies, but also on the Mexican spotted owl (e.g., see reviews in Ganey and Dick 1995 and Gutiérrez et al. 1995). Early studies by Ganey and Balda (1989a, 1994) linked the Mexican spotted owl with late seral stage forests where the owl occurred outside of canyon habitats. These early Mexican spotted owl habitat studies set the stage, as it did for the northern and California spotted owls, for the seemingly inevitable conflict over the effect of logging on the owls. In the southwestern United States this conflict transpired much more quickly than it did for the northern spotted owl, but unlike the northern subspecies the initial petition to list the Mexican subspecies was accepted (USDI 1993). The primary basis for listing the Mexican subspecies was past and potential habitat loss, as well as the failure of existing

regulatory mechanisms to protect the bird (i.e., land management and regulatory agencies could not reach agreement on a proactive plan to prevent listing; USDI 1993). A contributing factor to uncertainty over the status of the owl was the lack of information on Mexican spotted owl population dynamics.

To address this lack of information, we began a long-term study of the population dynamics of the Mexican spotted owl at 2 sites, 1 in north-central Arizona and 1 in west-central New Mexico. Our strategy was to develop baseline information on habitat relationships and natural history of these 2 populations, which we could ultimately link with population characteristics. Our habitat studies were centered at both territory (Seamans and Gutiérrez 1995, May et al. *In Press*) and landscape scales (Peery et al. 1999, May and Gutiérrez 2002). Spotted owls in our 2 study areas exhibited different habitat use patterns, probably because there was more mixed conifer habitat on the New Mexico study area than on the Arizona study area (Peery et al. 1999, May and Gutiérrez 2002). Nevertheless, mixed conifer habitats were very important in Arizona despite being relatively rare (May and Gutiérrez 2002). In addition, the presence of large oaks (>45.7 cm dbh) appeared to be a key habitat element within the pine-oak habitats in Arizona (May and Gutiérrez 2002), whereas they did not exist as a key feature in habitat used by owls in New Mexico.

Our study populations declined over the early years of study (Seamans et al. 1999). They also showed considerable variation in vital rates during the first 8 years of study; reproduction showed strong temporal fluctuations correlated with climate conditions

whereas survival did not show such strong relationships (Seamans et al. 2002). Studies of northern and California spotted owl populations have demonstrated a strong relationship between reproduction and climate (Franklin et al. 2000, LaHaye et al. *In Review*, respectively). However, the Mexican spotted owl populations we studied were exposed to more complex precipitation patterns (both winter precipitation and summer monsoon) than those influencing coastal populations (winter precipitation followed by a dry summer). Thus, these climate patterns may have different influences on prey populations and owl energetic constraints. Although annual reproductive output was correlated between our 2 study areas, annual survival rates were only weakly correlated (Seamans et al. 2002). Thus, our study provided an opportunity to evaluate the effects of climate and habitat on these 2 owl populations occupying different habitat and landscapes.

Noon and Franklin (2002) stressed the need to explain mechanisms for habitat effects on vital rates. Effective management of forests for spotted owl persistence will depend on knowledge of how demographic rates can be affected by the types and amounts of habitat present within owl territories. Natural resource managers could use such information when establishing target conditions for specific forest stand structure, or for the composition of forest types at the landscape scale. Thus, our analyses included habitat covariates that we considered relevant to spotted owl biology and that resource managers could use to develop and maintain spotted owl habitat.

Our specific goals were to (1) estimate survival and reproductive rates of owls in these populations, (2) examine the effects of climate and habitat on owl demographic parameters

(survival, reproductive output, and recruitment) using a model selection approach, (3) use components of variation analysis to estimate the amount of temporal and spatial process variation explained by climate and habitat variables, respectively, (4) estimate the population rate of change to examine trends in owl numbers, and (5) provide recommendations to improve the management of forests for Mexican spotted owl survival and reproduction. We developed an extensive suite of *a priori* hypotheses (i.e., models) to evaluate relationships of interest, and we explain these in detail below. We conducted separate analyses for each study area.

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METHODS

Study Areas

We studied Mexican spotted owl populations on 2 study areas, 1 in north-central Arizona and 1 in west-central New Mexico (Fig. 1), from 1991 to 2002. We do not know the criteria used for selection of the initial study areas because they were selected by the U.S. Forest Service *a priori* and included in a Research Funding Proposal solicitation. However, the management history, topography, climate, and vegetation differed between the study areas. The Arizona study area encompassed 585 km^2 of the Coconino Plateau and was located 40 km southeast of Flagstaff, Coconino County, Arizona. The U.S. Forest Service was the primary land manager, managing the area for recreation, livestock grazing, and timber harvesting. The primary timber harvest technique was selective cutting (Smith 1962), and most (i.e., >90%) of the forest had been logged in the past. The topography was generally flat with several small, forested cinder cones. Elevation ranged from 1,800-2,660 m. The climate was characterized by warm summers and cold winters (Fig. 2a).

Precipitation primarily occurred December–March as snow; however, monsoon thundershowers were common from early July–September (Fig. 2a). We changed the boundary of the Arizona study area after the 1991 field season because the original delineation of the study area included vast areas of unsuitable habitat (e.g., grassland, piñon-juniper [*Pinus edulis-Juniperus* spp.] woodland), which resulted in inefficient survey effort (i.e., large areas surveyed did not harbor owls) and an insufficient number of owls to allow precise estimation of vital rates. The study area boundary was reduced on the northeastern side and expanded on the northwestern side, where potential spotted owl habitat existed.

The New Mexico study area encompassed 323 km^2 of the Tularosa Mountains and was located 10 km northeast of Reserve, Catron County, New Mexico. The U.S. Forest Service was the primary land manager, managing the area for livestock grazing, timber harvest, and recreation. However, recreation and public use of this study area was considerably less than on the Arizona study area (e.g., the Arizona study area served as the summer weekend retreat for hundreds to thousands of Arizona urbanites). Shelterwood cutting (Smith 1962) was the primary timber harvest method; approximately 30% remained as unlogged or mostly unlogged forest. The topography was characterized by moderate- to steep-sloped canyons, with elevations ranging from 1,900-2,900 m. The climate was slightly warmer than the Arizona study area (Fig. 2b). Most precipitation occurred July–September as monsoon thundershowers, with occasional snow during winter (Fig. 2b).

Forest communities on both study areas were similar though they differed in relative

abundance. Mixed conifer forest (4.8% and 28.5% of Arizona and New Mexico, respectively), present at higher elevations and on north-facing slopes, was dominated by Douglas-fir (*Psuedotsuga menziesii*) and white fir (*Abies concolor*) but included ponderosa pine (*Pinus ponderosa*), quaking aspen (*Populus tremuloides*), and Gambel oak (*Quercus gambelii*). Pine-oak forest (78.3% and 45.3% of Arizona and New Mexico, respectively) was dominated by ponderosa pine and Gambel oak, and occurred at mid-elevations and on south-facing slopes. Lower elevations consisted of grasslands (15.8% and 3.2% of Arizona and New Mexico, respectively) and piñon-juniper woodland (1.1% and 23.0% of Arizona and New Mexico, respectively), which was dominated by piñon pine (*P. edulis*) and junipers (*Juniperus deppeana* and *J. monosperma*).

Field Effort

Surveys and monitoring.—During each breeding season (Apr–Aug) from 1991 through 2002, we used standard techniques to locate territorial spotted owls and their nests and roosts (Franklin et al. 1996a, Seamans et al. 1999). We surveyed each study area ≥2 times each year using a combination of permanent survey points and survey routes in areas where points were not practical (e.g., remote canyons with no road access). In addition, we surveyed historical owl territories each year. We located owls using vocal imitations of their calls to elicit responses (Forsman 1983). After eliciting a response from an owl, we conducted additional surveys to estimate occupancy and reproductive status of territories and to locate nests and roosts. We distinguished the sex of responding owls based on their calls or behavior; males had a lower pitch call and only females incubated eggs (Forsman et

al. 1984). We recognized 4 age classes based on plumage characteristics: young of the year, 1-year-olds, 2-year-olds, and ≥3-year-olds (Moen et al. 1991). We did not determine the sex of juveniles because a reliable field technique did not exist.

Each year, we attempted to identify every territorial spotted owl and fledged young on each study area. We used a variety of methods to capture owls, including noose poles, snare poles, bal-chatri traps, and mist nets (Forsman 1983, Bull 1987). We banded each owl with a U.S. Fish and Wildlife Service (USFWS) numbered, locking aluminum leg band. In addition, we color banded owls to facilitate subsequent identification of individuals (Franklin et al. 1996a). We used a unique color combination for each territorial owl, but we banded all young fledged within a given year using identically colored bands (i.e., cohort bands). After initial capture, we identified owls during subsequent years by resighting color bands or by physically recapturing individuals and recording their USFWS band number. We physically recaptured owls to replace worn color bands or cohort bands on individuals that had survived their first year. Band loss was minimal using these color bands (Forsman et al. 1996b).

We estimated the reproductive output of territorial owls by feeding them live mice (*Mus musculus*; Forsman 1983, Franklin et al. 1996a). Typically, breeding spotted owls take prey to the nest or fledged young whereas non-breeding owls eat or cache prey. We used a minimum of 2 mice to assess annual reproductive output, which we defined as the number of young fledged by each territorial pair (see Petersburg et al. *In Review* for a statistical analysis of the efficacy of our protocol). If 1 member of an owl pair ate or cached 2 mice

sequentially between 1 June and 15 July, and no juveniles were detected, then we assumed no young had fledged. If fledglings were detected, we then fed the owl ≥2 additional mice to estimate the total number of young fledged. If we detected young but <4 mice were taken during a given visit, we returned to the territory at a later time to try to satisfy the mousing protocol. We visited owl pairs as many times as necessary to assess reproductive output. Our results using this 2 mouse protocol were consistent with those obtained using the 4 mouse protocol used in previous analyses (e.g., Seamans et al. 1999, Petersburg et al. *In Review*). For example, considering data collected between 1 June and 15 July for both study areas and across all years (n = 583 visits), the 2 mouse protocol yielded results identical to the 4 mouse protocol in 98% of the cases in which we found juveniles (Petersburg et al. *In Review*). However, the 2 mouse protocol had the added advantage of increasing the sample size of non-breeding pairs for which we obtained reproductive output data. Occasionally, an owl or pair of owls would not take mice under any circumstances. If this occurred, we assumed a pair did not fledge young if a female ignored mice for >1 hour and we did not observe her on a nest between 10 May and 1 June, and we did not hear or observe young in the territory between 1 June and 15 July.

Biological Hypotheses, Predictions, and *A Priori* Model Development

We developed a suite of *a priori* hypotheses to examine the effects of climate and habitat on demographic parameters. We first expressed our conceptual hypotheses as verbal hypotheses. We then translated each verbal hypothesis into a quantitative candidate model to be used within an information theoretic model selection framework (Burnham and

Anderson 1998). Because more habitat studies have been published on spotted owls than any other raptor (Lõhmus 2003), we benefitted from many potential extant hypotheses about the relationships between habitat characteristics and spotted owls. In addition, the effect of weather or habitat on the vital rates of spotted owls had been investigated by Franklin et al. (2000), Seamans et al. (2002), and LaHaye et al. (*In Review*). Thus, we selected relevant and potential elucidating hypotheses from among these previous investigations. We developed additional hypotheses by searching published papers on a variety of topics related to spotted owl biology, other raptors (both diurnal and nocturnal), general avian ecology, and small mammals. We generally limited our search of small mammal literature to the primary prey of the Mexican spotted owl. Finally, based on our experience and knowledge of spotted owls and the study areas, we developed additional candidate models for consideration.

Biological basis for delineating important time periods of the spotted owl annual cycle.—We hypothesized that the annual life cycle of the owl included time periods that were critical to population processes. We used these time periods to facilitate model development. Our rationale for the biological basis of critical time periods that affect Mexican spotted owl population dynamics followed Franklin et al. (2000) and Seamans et al. (2002). Our specific hypotheses (Table 1) followed from the general logic outlined below. Because this was not an experimental study, we viewed these hypotheses as a set of plausible, competing alternatives regarding the potential direct or indirect effects of weather or habitat factors on different life history characteristics. In a given year (t), we

assumed that winter (1 November [t-1] to 31 March [t]) was a critical period for both survival and reproduction. We hypothesized that stress during winter could result from depressed prey populations, reduced foraging efficiency due to prey inaccessibility and weather, or increased metabolic requirements of owls, which could affect reproduction or survival rates. For reproduction, we hypothesized that both the early nesting (1 April [t] to 15 May [t]) and late nesting (16 May [t] to 15 June [t]) periods were potentially critical. For example, during the early nesting period, females brood the eggs and rely on their mates to deliver food. Consequently, low prey numbers or inclement weather could affect the ability of males to find or capture prey, which would reduce prey delivery rates to females. Such a reduction in prey delivery rates would force females either to abandon nests or to leave nests to search for food themselves, which could reduce nesting success during this period by allowing exposure of eggs to inclement weather or predators. Food abundance or availability could be critical for successful reproduction in the late nesting period when juveniles are developing and fledging. Inclement weather during this period could be detrimental to juvenile survival if females cannot brood young or if the young receive insufficient food. In addition, young may be more vulnerable because food begging vocalizations and increased movement may attract predators.

Climate model development.—We developed a suite of *a priori* climate models (Table 1) by hypothesizing how ambient temperature or number of precipitation days during critical time periods might affect vital rates. Climatic factors (i.e., temperature and precipitation) could influence raptors directly by increasing their energetic demands or by

limiting their ability to obtain food (Cavé 1968, Newton 1978; also see discussions about spotted owls by Franklin et al. 2000, North et. al 2000, Ward 2001, Seamans et al. 2002). Effects may also be indirect through impacts on primary productivity, which would affect prey abundance, or prey abundance per se (see discussions by Franklin et al. 2000, Ward 2001, Seamans et al. 2002). Primary prey of Mexican spotted owls included white-footed mice (*Peromyscus* spp.), woodrats (*Neotoma* spp.), and voles (*Microtus* spp.) (Ganey et al. 1992, Seamans and Gutiérrez 1999, Ward 2001). Common forage of these prey species included forbs, grass seeds, and tree seeds (Jameson 1952, Goodwin and Hungerford 1979). Because growth of these forage plants depends upon moisture, we hypothesized that precipitation during the past year (November–October; Table 1, model S1) or previous year (model S2) may positively influence spotted owl survival through effects on primary production and prey abundance. These models examined a linear relationship between annual precipitation and survival. Alternatively, the effect of precipitation on survival may have been in the from of a pseudothreshold (see Franklin et al. 2000); that is, increased precipitation may have benefitted spotted owls up to a point, beyond which the benefit leveled off (models S3 and S4). Because spotted owls hunt primarily by sound (Forsman et al. 1984), increased winter precipitation may have negatively affected the foraging ability of spotted owls by reducing prey detectability (e.g., through the background noise of rainfall or by providing prey with a protected subnivean environment). In addition, wet winter conditions may have depressed overwinter small mammal populations on our montane, temperate study areas (Sleeper 1979). Therefore, we hypothesized that winter

precipitation would negatively influence survival (model S5). Alternatively, precipitation during the previous winter (i.e., year *t-1*) may have positively affected survival by increasing spring primary production, which may have increased prey reproduction during the summer, thereby resulting in higher prey abundance during the following winter. We hypothesized that this effect of precipitation during the previous winter could take either a linear (model S6) or pseudothreshold (model S7) form (Franklin et al. 2000). We also examined an interaction effect between winter precipitation and low temperature (model S8). In this model, we hypothesized that increased precipitation and temperatures could have affected owl survival, but the slopes of the effects might be different. For example, precipitation could have had a greater effect on survival when the temperature was high because precipitation would have occurred in the form of rain, which would have greater heat dissipation qualities (i.e., affecting owl thermoregulation) than snow.

On our study areas, monsoon rain usually occurred from July–September and could be a significant source of annual precipitation. Dry monsoon years could reduce late summer primary productivity (Ernest et al. 2000), which could limit late season prey reproduction and overwinter abundance. Drought conditions during the monsoon season could inhibit the maturation of acorns (McPherson 1992, McCraken et al. 1999, McShea 2000) and reduce the survival of Gambel oak (Harper et al. 1985). Gambel oak was an important food resource for prey populations (Finley 1958) and was a documented habitat associate of Mexican spotted owls (Ganey and Dick 1995, Hodgson 1996, Ganey et al. 1999, May and Gutiérrez 2002, May et al. *In Press*). In addition, low monsoon precipitation may have

increased the destruction of stored tree seeds by insect larvae (Neilson 1981, Harper et al. 1985), which could reduce the overwinter food supply for seed-storing rodents. Therefore, we hypothesized that a dry monsoon season would negatively impact survival the following year (model S9). Because spotted owls may depend on precipitation during more than 1 period, we hypothesized that both monsoon and winter periods may be important to survival (model S10). We also examined the effect of drought (or wet) conditions using the Palmer Z Index (Palmer 1965; see *Climate covariates* below for a description of this covariate). Because drought affects food abundance (Neilson and Wullstein 1983, Sork et al. 1993) and subsequent reproduction of prey populations (Nelson 1993), we hypothesized that dry conditions during spring and summer (1 March–30 September) would negatively influence owl survival over winter (model S11). We used the Palmer Z Index to represent dry (or wet) conditions as expressed in model S11.

We hypothesized that climate might influence spotted owl reproduction in many of the same ways we predicted for survival above. However, for reproduction, the suggested effects may extend to owl nestlings and fledglings, or impact the capability of the parents to provide food for their young. For example, dry conditions during the winter months prior to nesting may have reduced spring forage, which subsequently reduced spring and summer prey abundance. In addition, egg follicle development in female raptors depends on fat reserves accumulated prior to clutch initiation (Newton 1979:105); therefore, spotted owl reproductive output probably was affected by female body condition prior to egg laying (around 1 April; Forsman et al. 1984, Delaney et al. 1999). We hypothesized that climate

patterns during the months before egg laying may have affected female body condition through direct (e.g., forging success) or indirect (e.g., prey abundance) mechanisms. Thus, we examined the effects of precipitation during annual (models R1 and R2), winter (model R3), and monsoon (model R4 and R5) periods on reproduction. We also hypothesized that reproduction may have varied with precipitation during the monsoon and winter periods combined (model R6) or with spring and summer moisture conditions (model R7).

Our suite of models also included hypothesized direct effects of climate on nesting spotted owls or their young. Cold and wet conditions during the nesting period negatively affected the reproductive success of spotted owls (Franklin et al. 2000, North et al. 2000) and other raptors (Kostrzewa and Kostrzewa 1990, Steenhof et al. 1997, Steenhof et al. 1999). During the early nesting (1 April–15 May) or late nesting (16 May–15 June) periods of spotted owls, embryos or nestlings may perish if exposed for a sufficient time to low temperatures or heat dissipation after becoming wet from rain or snow. In addition, cold, wet conditions during nesting may have reduced the foraging success of owls (see Cavé 1968, Newton 1978); if a male failed to provision the female adequately, she may have left the nest to forage for herself. Thus, we hypothesized that increased precipitation during the early nesting period (model R8), late nesting period (model R9), and both periods combined (model R10) would negatively affect reproduction. We also hypothesized that cold, wet conditions during the early nesting period could have negatively affected reproduction either by an additive effect (model R11) or by an interaction effect between the precipitation and temperature covariates (model R12).

Finally, we predicted that increased precipitation during the previous monsoon and winter periods in combination with warm temperatures during the early and late nesting periods could have positively affected owl reproduction (model R13). This model represented a combination of long-term precipitation effects and short-term temperature effects.

Habitat model development.—We developed a suite of *a priori* habitat models (Table 2) to explore the effects of different habitat types and landscape metrics on spotted owl vital rates. The relationship between spotted owls and mature forest has been described extensively in the literature (Forsman et al. 1984, Ganey and Balda 1989a, Bart and Forsman 1992, Thome et al. 1999, Franklin et al. 2000, Ward 2001). Mexican spotted owls selected mature, unlogged forests over managed forests for foraging and roosting (Ganey and Balda 1994). Stands of unlogged forest were present in 97% of owl sites in northern Arizona (Ganey and Balda 1989b). The amount of late seral forest has been positively correlated with northern spotted owl productivity (Bart and Forsman 1992, Thome et al. 1999). Old forest structure, which includes logs and snags, may provide nesting and hiding cover for key owl prey species (Goodwin and Hungerford 1979, Ganey 1992, Ganey and Balda 1994, Ward 2001). In addition, Forsman et al. (1984) and Gutiérrez (1985) hypothesized that old forests may provide more nesting sites than younger forests; if this were true, reproductive potential may be limited in younger forests. Both northern and Mexican spotted owls selected nest and roost sites primarily in mature mixed conifer forest (Seamans and Gutiérrez 1995, Swindle et al. 1999). Therefore, we hypothesized that the amounts of mature forest and mature mixed conifer forest within a spotted owl territory

would benefit both survival (Table 2, models S1 and S2) and reproduction (models R1and R2). In New Mexico, spotted owls occupied sites with more mature mixed conifer forest and mature pine forest than expected, whereas they were not found in large areas of younger forest (Peery et al. 1999). Ganey and Balda (1994) reported that telemetered owls consistently avoided managed forests. Thus, we predicted that more young forest in the territory would negatively affect survival (model S3).

Of 4 vegetation communities examined during a New Mexico study of spotted owl habitat, mixed conifer forest had the lowest prey biomass during winter (Ward and Block 1995). Prey biomass in mixed conifer forests may have affected owl survival during winter. Thus, we hypothesized that the amount of mixed conifer forest (regardless of seral stage) in an owl territory could negatively influence survival (model S4). Prey biomass also may have affected the condition of females prior to courtship and nest initiation, which in turn may have influenced egg-laying. White et al. (1995) suggested that reproductive rates of Mexican spotted owls may decrease with increased amounts of mixed conifer forest. In Arizona, where only 3% of the forest was mixed conifer, 51% of owls located were found in mixed conifer habitat (Ganey and Balda 1989b). In another Arizona study, mixed conifer forest comprised 5% of the study area, but owl sites contained 82% of available mixed conifer habitat (May and Gutiérrez 2002). Thus, we included models exploring both positive and negative effects on reproduction (models R3 and R4) due to the contradictory evidence presented in the literature.

Mexican spotted owls also have been associated with pine and pine-oak forests. Forty

percent of spotted owl nests in central Arizona were located in mature Gambel oak trees in pine-oak forest stands; another 37% were in ponderosa pine trees (May et al. *In Press*). Other studies have documented extensive use of oaks for nesting and roosting by spotted owls (Ganey and Dick 1995, Steger et al. 1997, Young et al. 1998). White et al. (1995) analyzed the percentages of forest types within 182 ha surrounding spotted owl locations and found positive correlations between (1) pine-oak forest and owl reproduction and (2) pine forest and owl persistence, an indirect measure of survival. Thus, we hypothesized that the amount of pine and pine-oak forest in an owl territory could have positively affected both survival (model S5) and reproduction (model R5).

For each study area, we defined an *other* habitat class, which consisted of all vegetation classes in which we did not observe a spotted owl nest or roost (*sensu* Franklin et al. 2000). White et al. (1995) detected a positive relationship between the percentage of unsuitable habitat (analogous to our *other* class) and Mexican spotted owl reproductive rates. Therefore, we hypothesized that territories that included larger amounts of *other* habitat could have higher reproduction (model R6).

Forest patch structure and diversity have also been positively associated with owl vital rates (Ward and Block 1995, Franklin et al. 2000, Ward 2001). Assuming that prey abundance varies by habitat and time, it follows that owls occupying territories composed of equal proportions of all habitat types used by owls would be more likely to survive fluctuations of a particular prey species (Ward and Block 1995, Ward 2001). Likewise, owls would be more likely to find enough food to reproduce when they have a diversity of

prey available and can forage opportunistically during peaks of species abundance or take advantage of non-synchronous prey cycles (Korpimäki 1988, Ward 2001). Therefore, we hypothesized that territories that included equal portions of vegetation types used by owls would have higher survival (model S6) and reproduction (model R7). We estimated this equability of habitats within a territory using a dominance metric (see *Covariate Estimation* below).

Franklin et al. (2000) reported that the best approximating models explaining variation in apparent survival and reproductive output of northern spotted owls included the total amount of primary spotted owl habitat and the amount of edge between primary spotted owl habitat and other habitats. Survival positively correlated with the total amount of primary spotted owl habitat, whereas reproductive output was negatively correlated with the same variable. Both survival and reproduction were positively correlated with amounts of edge. Thus, we predicted that the total amount of primary spotted owl habitat (see *Covariate Estimation* below for a definition of primary spotted owl habitat), larger patches of primary spotted owl habitat, and increased amounts of edge between primary spotted owl habitat and other habitats would positively affect survival of Mexican spotted owls. We examined models containing each of these 3 covariates alone (models S7-S9) and combined in 1 model (model S10). We predicted that reproduction would be negatively affected by the total amount of primary spotted owl habitat (model R8), but positively affected by larger patches of primary spotted owl habitat (model R9) and increased amounts of edge (model R10). Finally, we examined the additive effects of these 3 covariates on

reproduction (model R11).

Covariate Estimation

Climate covariates.—We used data from 3 weather stations (Western Regional Climate Center 2002) on or near each study area to calculate climate covariates. We selected weather stations that represented the areal extent and elevation range of each study area. Climate covariates were calculated separately for each year and each study area. We felt the frequency of precipitation was more important than the total amount; therefore, we used the number of days with measurable (0.03 cm) precipitation during a particular time period of the annual cycle for analyses. We calculated the number of precipitation days at each weather station during the period of interest. We then averaged these values across weather stations to produce a variable representative of the entire study area. Precipitation days were correlated with absolute precipitation (Arizona: $r = 0.66$-0.97, $df = 9$, P 0.02; New Mexico: $r = 0.87$-0.97, $df = 9$, $P < 0.001$). For temperature covariates, we averaged the minimum temperatures for all days during a period of interest at each weather station. We then averaged the values across stations to produce a variable representative of the entire study area.

We used the Palmer Z Index (ZNDX; Palmer 1965) to produce a covariate of moisture conditions. The ZNDX is based on a water budget model for soil moisture and includes components for precipitation, evapotranspiration, soil moisture loss and recharge, and runoff (Palmer 1965). The ZNDX is computed monthly for regions within each state (National Climate Data Center 2002) and is sensitive to short-term deviations in moisture

condition during otherwise long-term trends (Karl 1986). We calculated a moisture covariate by averaging the monthly ZNDX values for each study area over the period of interest, March–September. Thus, this covariate reflected short-term deficits or excesses in soil moisture conditions during the spring and summer months. During the period of our study, the ZNDX was correlated with the commonly used Palmer Drought Severity Index (Arizona: $r = 0.77$, df = 9, $P = 0.002$; New Mexico: $r = 0.90$, df = 9, $P < 0.001$; Palmer 1965).

Habitat covariates.—We used a 1.1 km radius circle to represent each spotted owl territory. This radius represented one-half the median nearest neighbor distance between owl territories on each study area during 1993, the year of highest owl density. We estimated a center point for each territory by calculating the geometric mean of all Universal Transverse Mercator (UTM) coordinates of owl nests and roosts within each territory. First we averaged locations within a year; then we averaged the annual locations to estimate a UTM coordinate representative of a given territory for the entire study period. Because spotted owls are central-place foragers (Carey and Peeler 1995), we gave priority to nest locations. For years when a nest location was available, that location was used as the annual territory center. When a nest location was not available, we averaged the locations of all unique roosts within the territory for a particular year. If a bird(s) was found on the same roost during multiple visits within a year, we only counted that roost location once. However, if the same roost was used in multiple years, it was used to estimate the annual territory center for each year it was used.

We estimated habitat covariates from landscape scale maps of vegetation cover types created for the Arizona (May and Gutiérrez 2002) and New Mexico (Peery et al. 1999) study areas. We used ArcView GIS 3.2 (ESRI 1996) and FRAGSTATS 2.0 (McGarigal and Marks 1995) to extract spatial data from the maps. We developed 2 categories of habitat covariates; 1 category was based on the area of vegetation classes within each owl territory while the other was based on landscape metrics within each territory (Table 3). To estimate 3 of the landscape metric covariates (SOEDG, SOMP, and SOCOR), we collapsed the vegetation classes on each study area into 2 broad categories, primary spotted owl habitat and other habitat. For each study area, we defined "primary spotted owl habitat" as any vegetation class in which we located a spotted owl nest or roost tree during the period of study; in general, this category consisted of closed canopy, mature forest. "Other habitat" consisted of vegetation classes that did not meet the criteria for primary spotted owl habitat. We calculated the core area (SOCOR) metric using a 30 m edge (Meyer et al. 2001); that is, a 30 m wide strip around the perimeter of a patch was subtracted from the total area of the patch to calculate the amount of core habitat contained in a given patch. We calculated 1 additional landscape metric, dominance (DOM), using the original vegetation classes (i.e., without collapsing them into 2 classes). Dominance provided an index of the evenness of vegetation classes within a given owl territory (*sensu* Meyer et al. 1998).

Data Analysis

We conducted the analysis of each vital rate in stages by examining subsets of the

hypothesized models in the following order: (1) models without climate or habitat constraints, (2) models with climate constraints only, and (3) models with habitat constraints only (see Franklin et al. 2000). This procedure allowed us to limit the total number of models examined. For example, our subset of models without climate or habitat constraints included both a hypothesized sex effect model (i.e., the estimated vital rate differed between females and males) and a "means" model (i.e., no difference between females and males). If the sex effect was supported by the data, we were able to retain it in all subsequent models that examined the effects of climate or habitat. Thus, we reduced the number of models we examined by half because we did not examine all subsequent models both with and without the sex effect. When modeling climate or habitat effects, we further limited the number of models considered by first examining simple linear relationships between covariates and population parameters. If a model containing a simple linear function was well supported (i.e., competing; see below), then we examined nonlinear relationships such as pseudothreshold and quadratic trends (G. White, personal communication). However, in some cases, we included nonlinear relationships in our *a priori* suite of models because our literature search or experience suggested such a relationship might explain the data.

We used Akaike's information criterion corrected for small samples (AIC_c) to rank candidate models (Hurvich and Tsai 1989, Burnham and Anderson 1998). We used AIC_c weights (Buckland 1997) and ΔAIC_c to assess model uncertainty and the likelihood of each model given the data. We calculated a 95% confidence set of models using AIC_c weights,

and we defined competing models as those within 2 AIC_c units of the top model (Burnham and Anderson 1998). We calculated the relative importance of a given variable by adding the AIC_c weights of all models containing the variable. We did not address multicollinearity *a priori* because we lacked a means to decide which covariates were more biologically meaningful from the owl's perspective. Instead, we addressed this issue when reporting model uncertainty by summing the AIC_c weights of models containing correlated covariates. We used Pearson product-moment correlation coefficients (Zar 1999) to assess collinearity. We considered variables with coefficient values >0.60 to be correlated.

Survival.—We compiled a capture history matrix for all banded territorial owls. Each row in the matrix represented the capture history for an individual owl and consisted of a series of 1s and 0s indicating whether an owl had been encountered (1 = yes, 0 = no) during a particular year. An encounter was defined as either a physical capture or a resight of an individual's uniquely colored leg band. For example, 1 would interpret the capture history 001101 to mean that the owl was first captured in year 3, recaptured/resighted in years 4 and 6, and not encountered in years 1, 2, or 5. We constructed separate capture history matrices for each study area. We did not estimate juvenile survival because potential bias associated with permanent emigration of dispersing juveniles could have resulted in an underestimate of this parameter (Franklin et al. 1996, Raphael et al. 1996).

To address the different objectives of our analyses (i.e., temporal versus spatial effects on survival), we constructed 2 versions of the capture history for each owl. For analyses involving temporal (i.e., time trends, climate) variation in survival, we made inferences

based on individual owls. Therefore, the capture history for an individual owl consisted of a single line of 1s and 0s which represented all encounters of the owl anywhere on the study area. For analyses involving spatial (i.e., habitat) variation in survival, our goal was to make inferences based on the habitat occupied by an owl, which varied by territory. Thus, we modified the capture histories used for the temporal analyses to reflect movement between territories (*sensu* Franklin et al. 2000). For each owl, we constructed a separate capture history (i.e., a separate line of 1s and 0s) for each territory occupied. Movement out of a territory was counted as a "loss on capture" (White and Burnham 1999). These modified capture histories allowed us to estimate survival probabilities associated with particular habitat covariates. We also used this technique for owls occupying 4 territories in New Mexico that experienced habitat change from the HB Wildfire in 1995. In these cases, while an owl may have occupied the same physical area both before and after the fire, we assumed the habitat had been altered sufficiently to affect the owl's survival probability. To quantify values of habitat covariates for the post-fire territories, we created a new ArcView coverage representing the extent of the HB Wildfire, which included both high and low intensity burn areas. We then subtracted the area that had been burned at high intensity (>35% canopy kill) in each territory from the pre-burn habitat class and added it to the OTHER class. For areas that burned at a low intensity (≤35% canopy kill), we did not make any adjustment because owls continued to use these areas for nesting and roosting (unpublished data).

We used the Cormack-Jolly-Seber open population model (CJS; Cormack 1964, Jolly

1965, Seber 1965) within Program MARK v3.0 (White and Burnham 1999) to estimate apparent survival and recapture rates of territorial owls. Estimation of true survival would require data on the emigration rate of spotted owls on our study areas; that is, an owl could have survived but left the study area and remained undetected. While we could not estimate emigration using our data, our estimates of apparent survival of territorial owls should be close to true survival because emigration by territorial spotted owls was probably uncommon (Raphael et al. 1996). We used Program RELEASE to assess goodness of fit (GOF) for the saturated model (Burnham et al. 1987) and to estimate , a measure of overdispersion (White 2002). Overdispersion of data can occur when observations are not independent. We estimated as χ^2/df, where both χ^2 and df were from TEST 2 + TEST 3 of Program RELEASE.

We first examined a set of *a priori* model structures for recapture rates. Recapture rates must be appropriately structured to provide valid inferences for survival, the population parameter of interest. We hypothesized that recapture rates remained constant during the study (denoted by "."). We also examined 3 temporal patterns: categorical (t), linear (lt), and quadratic ($t+t^2$). When owls were nesting, we observed that they took mice more readily, making them easier to resight and capture. Therefore, we hypothesized that recapture rates fluctuated with the proportion of pairs nesting (N). We examined an age effect (a2) structure which assumed that subadult (<3 years old) owls were easier to capture and resight than adult (≥3 years old) owls. Finally, we hypothesized that recapture rates varied with the project leader (PL) because multiple project leaders, or field supervisors,

worked on each study area, and they varied in their experience working with spotted owls. We used AIC_c to determine the best model. Once we identified the best model structure for the recapture rates, we used this structure in the survival modeling.

In addition to climate and habitat covariates, we examined the effects of age (a2), sex (s), and time (t, lt, $t+t^2$) on survival. We also modeled linear combinations of these effects (e.g., s+lt). The age effect (a2) assumed that subadult (<3 years old) owls had lower survival than adult (≥3 years old) owls (Forsman et al. 1996a). We incorporated climate covariates into the analysis by entering the covariate values directly into the design matrix of Program MARK (White and Burnham 1999). We included habitat covariate values in the input files of Program MARK by associating a set of values, representing a particular territory, with each row of the capture history matrix, which represented an individual owl that had occupied that territory. We then accessed a particular covariate by specifying its name in the design matrix of Program MARK (Franklin 2002). Because Program MARK may fail to reach numerical convergence using large values for covariates, we transformed all precipitation and temperature covariates by dividing the raw values by 100. We scaled most habitat covariates to facilitate numerical convergence in Program MARK as well (Table 3). However, we back-transformed all covariate values (including their SE and confidence intervals) when presenting results to reflect the true relationships between covariates and population parameters.

Reproductive output.—We used mixed model analysis of variance (PROC MIXED in SAS; Littell, et al. 1996) to examine the effects of time, female age, sex, weather, and

habitat on reproductive output of Mexican spotted owls. We defined reproductive output (R), the response variable, as the number of fledged young per pair, which ranged from 0 to 4 (only 1 Arizona pair fledged 4 young). We only used pairs for which we estimated reproduction based on feeding 2 mice to a territorial owl (Petersburg et al. *In Review*). We considered female age, climate, and habitat covariates to be fixed effects. We considered territory and year to be random effects. Because reproduction within a territory among years may not be independent, we considered territory to be a random blocking factor. We treated year as the experimental unit in a repeated measures design because we were examining the effects of climate by year.

Valid inferences from our modeling results depended on selection of an appropriate variance-covariance (v-c) structure for each data set. Therefore, before examining our *a priori* models, we used a restricted maximum likelihood (REML) procedure to model the following potential v-c structures: compound symmetric, first-order autoregressive, heterogeneous first-order autoregressive, and log-linear (Littell et al. 1996). We used a REML procedure because it estimated the v-c structure after accounting for the fixed effects of the model (Searle et al. 1992), and our interest was the v-c structure of a random effect (i.e., year). Using AIC_c, we selected the v-c structure best supported by the data in each analysis. Once we identified an appropriate v-c structure, we used a maximum likelihood procedure to estimate the influence on R of the fixed effects (i.e., climate and habitat) in each hypothesized *a priori* model. Overdispersion was not a problem; therefore, we used AIC_c for model selection. We used the same scaling factors for climate and

habitat covariates in SAS that we used in Program MARK to facilitate numerical convergence of the estimation procedure. Again, we back-transformed all covariate values (including their SE and confidence intervals) when presenting results.

Model validation using 2002 reproductive output.—We attempted to validate our modeling procedure by predicting 2002 reproductive output (R) in both Arizona and New Mexico using the 95% confidence sets of climate models from our initial modeling analysis. When modeling reproductive output from 1991 through 2001, we were able to evaluate parameters that specified differences in owl age and temporal variation in reproduction. However, in order to make predictive statements regarding reproductive output during 2002, we limited model structures to parameters available prior to data collection (i.e., removed age and time constraints). Predictions were based on the following general model form:

Reproductive Output (R) = $\beta_0 + \beta_1 X_1 + \beta_2 X_2 \ldots \beta_k X_k$

where β = parameters, X = climate variables, and k = number of independent variables associated with each model. We calculated an expected (i.e., predicted) reproductive output estimate for 2002 as

$$= \sum_{i=1}^{n} R_i w_i$$

$$E(R)$$

where R_i = reproductive output predicted by model i, w_i = AIC_c weight of model i, and n = all models in the 95% confidence set of the analysis of data for 1991-2001.

Recruitment.—We estimated recruitment (*f*; the number of new animals that enter the territorial population at time *i* per territorial animal in the population at time *i*-1) using the Pradel survival and recruitment analytical approach (Pradel 1996) within Program MARK v3.0 (White and Burnham 1999). This structure does not incorporate age effects, therefore we limited our analysis to the effects of sex and time. New recruits can come from 3 sources: juveniles produced the previous year, immigration, and nonterritorial floaters (Franklin 1992). We incorporated climate covariates into the recruitment analysis using methods described in *Survival* above. However, we did not report recruitment for the first 2 years of study due to known bias resulting from a sampling "learning curve" and the change of the Arizona study area boundary in 1992 (see *Population rate of change* below and Hines and Nichols 2002). We did not investigate the effects of spatial (i.e., habitat) covariates on recruitment because of the loss of data resulting from splitting capture histories of individual birds that changed territories during the study period. In addition, owls recruited into the population would not be affected by habitat in a given territory the same way that owls would be affected by climatic conditions across the study area.

Components of variation.—We used variance components analysis (Searle et al. 1992) to estimate the amount of temporal and spatial process variation explained by climate and habitat variables, respectively, in high ranking models. We conducted components of variation analyses for survival models using Program MARK (White et al. 2002). We used a model without time constraints (i.e., ϕ_t) to estimate the amount of temporal process variation ($^2_{temporal}$) in survival. We then used a random effects model in Program

MARK to estimate the amount of $^2_{temporal}$ not explained (i.e., $^2_{residual}$) by the climate covariate(s) of the best climate model (White et al. 2002). Finally, we calculated the amount of temporal process variation explained by the climate covariate(s) as $^2_{climate} = ^2_{temporal} - ^2_{residual}$. We conducted components of variation analyses for recruitment using an identical methodology and output from Program MARK.

We used a similar methodology to estimate the components of spatial variation for survival. We used model $\{\phi_{territory}, p_{territory}\}$ to quantify the amount of spatial process variation ($^2_{spatial}$) in survival across spotted owl territories on each study area. We used a random effects model to estimate the amount of $^2_{spatial}$ not explained (i.e., $^2_{residual}$) by the habitat covariate(s) of the best habitat model (White et al. 2002). We calculated the amount of spatial process variation explained by the habitat covariate(s) as $^2_{habitat} = ^2_{spatial} - ^2_{residual}$.

Components of variation analyses for reproductive output models followed the general methodology used for survival and recruitment. We estimated $^2_{temporal}$ and $^2_{spatial}$ using an intercepts only model (i.e., R.) in PROC MIXED of SAS (SAS Institute 1999). We used the best climate model to estimate the amount of temporal process variation not explained (i.e., $^2_{residual}$) by the climate covariate(s). We then calculated the amount of temporal process variation explained by climate covariates as $^2_{climate} = ^2_{temporal} - ^2_{residual}$. Likewise, we used the best habitat model to estimate the amount of spatial process variation

not explained by the habitat covariate(s), and then we calculated the amount of spatial process variation explained by the habitat covariates as $^2_{habitat} = {}^2_{spatial} - {}^2_{residual}$. We used REML to estimate the variance components after accounting for the fixed effects in the model. We calculated confidence intervals for process variation following equations from Burnham et al. (1987:212).

We estimated coefficients of process variation for all population parameters as

$$\frac{\sqrt{\hat{\sigma}^2_{process}}}{\hat{\bar{\theta}}}$$

where $^2_{process}$ was either temporal or spatial process variation, and was the weighted mean of the population parameter of interest (Franklin et al. 2000:559). We used coefficients of process variation to estimate the degree of variation in a parameter over time or space.

Population rate of change.—We used different techniques to estimate population rate of change (λ) on the 2 study areas. For Arizona, we used the reparameterized Jolly-Seber (λ_{RJS}; Pradel 1996) method; we used λ_t to denote the annual estimates of λ. Franklin et al. (2003) discussed the benefits of, and appropriate inferences to be drawn from, λ_t compared to estimating λ using a projection matrix approach. To estimate λ_t, we used model $\{\phi_t, p_t, \lambda_t\}$ as the base for random effects modeling implemented in program MARK. In addition

to a fixed effects model (λ_t), we examined 3 random effects models: a means model (λ.), which assumed constant λ over time; a linear trend (λ_{lt}); and a quadratic trend (λ_{t+t^2}). We excluded the first estimable λ_t from our analyses. This λ was potentially biased due to trap response (Hines and Nichols 2002) and an increased efficiency (i.e., learning curve) in sampling as personnel became familiar with spotted owl survey and capture techniques during the early years of study. We had additional justification for excluding the first estimable λ_t from our analysis of the Arizona data because the study area boundary was altered in 1992 to encompass more potential owl habitat (i.e., owls; see *Methods* above). Estimation of λ_t assumed that the study area was consistently and thoroughly surveyed during the period for which λ was estimated (Franklin 2002, Hines and Nichols 2002). If the entire study area was not surveyed, an estimated change in λ could have been due to either a change in the number of owls sampled (e.g., more owls were present because the study area boundary increased) or a change in the number of owls in the previously sampled area (i.e., actual population growth).

For New Mexico, we were unable to use λ_t because the full model $\{\phi_t, p_t, \lambda_t\}$ failed to reach numerical convergence in Program MARK; that is, Program MARK failed to estimate the λ_t. We could not determine the root cause of this failure to numerically converge. Thus, we used an alternative approach, which used results from the survival and recruitment analysis to estimate λ. We used the model averaging feature of Program MARK (White et al. 2002) to obtain average annual survival and recruitment estimates

weighted by AIC_c weights for each parameter. We only used models in the 95% confidence set of the analysis. We calculated λ in a given year as $\phi_i + f_i$, where ϕ_i and f_i are model averaged apparent survival and recruitment in year *t*, respectively.

Annual estimates of λ may be difficult to interpret because, as the population fluctuates over many years, 1 has no reference value to indicate if the population is larger or smaller than it was in the initial year. Therefore, to facilitate interpretation of the annual estimates of λ, we calculated estimates of "realized change" for each population (Franklin et al. *In Press*). These estimates of realized change (Δ_t) represented the proportion of the original population that remained in year *t* and was calculated as:

$$\hat{\Delta}_t = \prod_{i=x}^{t-1} \hat{\lambda}_i$$

where x = the first estimated λ_t (Franklin et al. *In Press*).

RESULTS

Population Dynamics of Spotted Owls in Arizona

Field effort in Arizona.—During 12 years of study, we conducted 13,375 hours of surveys and located 63 unique spotted owl territories. We located owls in 45 (71%) of these territories in 1993, the year of highest occupancy, but only 19 (30%) territories were occupied in 1997 and 1998, the years of lowest occupancy (median across all years = 29 occupied territories). We banded 133 territorial owls (including 49 owls that we originally

banded as juveniles) and 198 juveniles. The age structure of the population fluctuated widely but males and females were evenly represented in each age class (Fig. 3). On average, 77.7% (SE = 3.9; range = 56.9, 100) of territory holders were adults (i.e., ≥3 years old) in any given year; the percentage of subadults in the territorial population ranged from 0% in 1995 and 1996 to 43.1% in 2000 (= 19.0%; SE = 4.3; Fig. 3). On average, 63.6% (SE = 8.91, range = 9.1, 100.0) of owl pairs nested in a year and, of those, 74.6% (SE = 8.61, range = 0.0, 100.0) fledged young. The percentage of pairs that fledged 0, 1, 2, or 3 young varied annually (Fig. 4). We recorded a complete reproductive failure in 2001; we documented 1 pair that fledged 4 young from a single clutch in 1999 (Fig. 4).

Effects of climate on owl survival in Arizona.—We estimated apparent survival and recapture rates based on the capture histories of 133 territorial owls (66 females, 67 males) banded from 1991-2001. The global model $\{\phi_{s*a*t}, p_{s*a*t}\}$ fit the data well ($\chi^2 = 11.41$, 31df, $P = 1.0$) and we found no evidence of overdispersion in the data ($\chi^2/df = 0.37$). The best supported recapture structure was $\{p_{t+t^2}\}$, which had an AIC_c weight of 0.845; there were no competing models within 2 AIC_c units. This structure indicated a quadratic trend over time, with the lowest recapture rate (0.861) occurring during the middle of the study (1996). The mean recapture rate across all years was 0.968 (SE = 0.0141). The 95% confidence intervals of all parameter estimates excluded 0. We maintained this model structure for recapture rates throughout subsequent survival modeling of climate and time effects.

Before modeling climate covariates, we examined the data for evidence of sex, age, and

time variation in survival rates. Of the 8 hypothesized models that we examined, the best (AIC_c weight = 0.743) model $\{\phi_t, p_{t+t^2}\}$ indicated that apparent survival varied over time with no consistent pattern (Fig. 5a); there were no competing models. In this model, we fixed the value of 1 parameter (ϕ for the interval 1992-1993) to 1.0. We fixed this parameters because all owls banded in 1992 were resighted or recaptured in 1993, resulting in a real estimate of 1.0. Because the logit link function used in Program MARK to estimate parameter values asymptotically approaches 1.0, the 1992-1993 ϕ would not be estimable without fixing the parameter. Because sex and age effects were not well supported (i.e., not competing models) at this stage of modeling, we did not include them in the subsequent analysis.

We considered 11 *a priori* hypothesized climate models (Table 1) in addition to the suite of sex, age, and time models examined above. Model $\{\phi_t, p_{t+t^2}\}$ remained the most parsimonious model based on AIC_c rank (Table 4). This model was 2.9 times more likely than the nearest model and had an AIC_c weight of 0.738. There were no competing models (i.e., ≤ 2 ΔAIC_c). The 95% confidence set did not include any models containing a climate covariate. However, model $\{\phi_{ZNDX}, p_{t+t^2}\}$ was the highest ranking climate model and indicated that spotted owl survival in Arizona was positively affected by wet conditions during the spring and summer prior to the winter survival interval (Fig. 5b). This model was ranked third and had an AIC_c weight of 0.007. The form of the relationship between survival and wet conditions in model $\{\phi_{ZNDX}, p_{t+t^2}\}$ was

$$= \frac{1}{1 + \exp[-(1.6349 + 0.5237 ZNDX)]}$$

where ZNDX was the average monthly moisture index during March–September of the previous year, $SE_{(0)} = 0.1393$ and $SE_{(ZNDX)} = 0.1117$ (95% CI = 0.3047, 0.7426). The top model was 105 times more likely than this moisture effect model, suggesting that the observed data in Arizona was not explained well by the climate variables we examined. Based on the coefficient of temporal variation, year-to-year variation in survival rates was low; the covariate for the moisture index in model $\{\phi_{ZNDX}, p_{t+t^2}\}$ explained about 52% of $^2_{temporal}$ in survival rates (Table 5).

Effects of climate on owl reproduction in Arizona.—Annual reproductive output (R) ranged from 0 to 1.83 fledged young per pair (= 0.94) and was based on 13-32 pairs/yr (total 238 pairs over 11 years in 50 territories). The v-c structure best supported by the data was compound symmetric, suggesting that variance in R was constant among years. We retained this v-c structure for all reproductive output models.

Before considering climate covariates, we examined 5 hypothesized models for effects of age and time variation on reproductive output. The most parsimonious model, $\{R_{female\ a2}\}$, indicated that mean reproductive output was greater for adult (≥3 years old) female owls (= 1.03; SE = 0.081) than for subadult (<3 years old) female owls (= 0.58; SE = 0.139). There were no competing models (AIC_c weight of model $\{R_{female\ a2}\} = 0.907$).

Though the data supported a female age effect on reproductive output, we did not include the a2 effect in the climate models because we did not locate any subadult female owls on the study area during 2 years (1996 and 1997). Thus, the effects of climate covariates on reproductive output of subadult females was unknown during those 2 years.

We examined 13 hypothesized climate models (Table 1). Model $\{R_{\text{female a2}}\}$ remained the most parsimonious model based on AIC_c rank and was 11.6 times more likely than the nearest model (Table 4). There were no competing models. Model $\{R_{ZNDX}\}$ was the highest ranked climate model, but was 36.8 times less likely than the top model based on AIC_c weight (Table 4). Model $\{R_{ZNDX}\}$ indicated that the reproductive output of owls was positively affected by wet conditions during the spring and summer months of the previous year (Fig. 6). The form of this model was

$$R = 0.8733 + 0.3053ZNDX$$

where ZNDX was the average monthly moisture index during March–September of the previous year, $SE_{(0)} = 0.1370$, and $SE_{(ZNDX)} = 0.1058$ (95% CI = 0.0707, 0.5400). Based on the coefficient of temporal variation, year-to-year variation in reproductive output was relatively high (Table 5). The moisture index explained about 42% of $^2_{\text{temporal}}$ in reproductive output, and variation due to sampling error was relatively low (Table 5). ZNDX was not correlated with any of the other climate covariates.

Model validation using 2002 reproductive output in Arizona.—In 2002, we randomly selected and surveyed 19 of the 26 territories occupied in 2001. We were unable to sample

all 26 territories due to time constraints. We estimated reproductive output at all but 1 sampled territory; therefore, we used survey results from 18 territories to compare the accuracy of the predicted estimate of reproductive output. Based on the weighted average of our *a priori* climate models, we predicted that owl reproductive output (R) in Arizona would be 1.06 fledged young per pair (Table 6). Our empirical reproductive output estimate for 2002 was 1.20 fledged young per pair. Thus, our models correctly predicted a relatively high R for Arizona, and the observed value fell within the range of predicted R estimates from the climate models (range = 0.76 - 1.43). In addition, though the average predicted reproductive output based on the 95% confidence set of models for the 1991-2001 data was very close to the observed empirical value, the predicted value using only the top model (R = 1.43) was higher than the observed 2002 reproductive output.

Effects of climate on owl recruitment in Arizona.—We used the best survival and recapture structures from the survival analysis (i.e., $\{\phi_t, p_{t+t^2}\}$) as a base for modeling recruitment (f). The global model fit the data ($\chi^2 = 18.47$; 25df; $P = 0.82$), and overdispersion was not evident in the data ($\chi^2/df = 0.74$). First, we examined the data for support of sex and time variation in recruitment. Of the 7 hypothesized models we considered, the highest ranked (AIC_c weight = 0.390) model, $\{\phi_t, p_{t+t^2}, f_{t+t^2}\}$, indicated a quadratic trend over time, with the lowest recruitment occurring during the interval 1996-1997 (Fig 7a). Model $\{\phi_t, p_{t+t^2}, f_t\}$ was about as likely (AIC_c weight = 0.353) as the top model and suggested that recruitment varied over time in no consistent pattern (Fig. 7a).

Based on this latter model (i.e., 1 with no time constraints), we estimated the mean annual recruitment rate during 1993-2000 to be 0.145 (SE = 0.0413, 95% CI = 0.064, 0.226) new territorial owls in year *t* per territorial owl in year *t*-1. A sex effect was not supported by the data and was not included in the climate models.

We examined an additional 7 models that related climate to spotted owl recruitment (Table 1). The original highest ranking models, $\{\phi_t, p_{t+t^2}, f_{t+t^2}\}$ and $\{\phi_t, p_{t+t^2}, f_t\}$, maintained their relative positions based on AIC_c (Table 4). The 95% confidence set of models did not contain any climate covariates. The highest ranked climate model was $\{\phi_t, p_{t+t^2}, f_{ZNDX}\}$, but it had an AIC_c weight of zero. This model suggested that recruitment was positively affected by wet conditions during March–September of the previous year (Fig. 7b). The form of this model was

$$\hat{f} = \frac{1}{\exp[-(-1.5498 + 0.2421ZNDX)}$$

where ZNDX was the average monthly moisture index during March–September of the previous year, $SE(_0) = 0.1032$ and $SE(_{ZNDX}) = 0.0866$ (95% CI = 0.0724, 0.4117). The moisture effect in this top ranked climate model explained about 32% of $^2_{temporal}$ in recruitment; 29% of the total variation in recruitment was due to sampling error (Table 5). The coefficient of temporal process variation for *f* suggested that the owl population experienced high year-to-year variation in recruitment (Table 5).

Population rate of change in Arizona.—We found no evidence of a clear trend in the λ_t analysis of the spotted owl population in Arizona. The most parsimonious model indicated a quadratic trend in λ_t (Table 7) with the population increasing during early and latter years of study and declining during the middle of the study period. However, when considering AIC_c weights, this quadratic model was about as likely as both the other models we considered (Table 7); 1 of these models suggested an increasing linear trend while the other suggested a constant rate of population change. In addition, the slope parameters for both the quadratic trend (β_t = -0.228; SE = 0.1449; 95% CI = -0.512, 0.056; β_{t^2} = 0.035; SE = 0.0210; 95% CI = -0.006, 0.077) and the linear trend (β_{lt} = 0.055; SE = 0.0399; 95% CI = -0.023, 0.133) were not different from zero based on the 95% confidence intervals. Annual estimates of λ_t ranged from 0.659 to 1.246. Mean λ from 1993 to 2000 (i.e., the years for which we estimated λ_t) was 0.995 (SE = 0.0814), which was not different from λ = 1.0 based on the 95% confidence interval (95% CI = 0.836, 1.155). Based on estimates of realized change (Δ_t), we calculated that 69.1% of the 1993 spotted owl population remained in 2000 (Fig. 8a).

Effects of habitat on owl survival in Arizona.—We banded 133 nonjuvenile spotted owls in 54 territories from 1991-2001. Of these banded owls, 109 occupied 1 only territory during the period that they were under observation, 19 occupied 2 territories, 4 occupied 3 territories (including 2 owls that occupied 1 territory during non-consecutive years, and occupied a second territory for ≥1 intervening year), and 1 occupied 4 territories. The

global model fit the data (χ^2 = 6.20, 20df, P = 0.99) and no overdispersion was evident (χ^2 /df = 0.31). Recapture structure $\{p_{t+t^2}\}$ best explained the data and indicated a quadratic time trend in recapture rates; rates declined to a low point during the middle (1996) of the study and then rose toward the end of the study. Confidence intervals for all parameter estimates for this recapture structure excluded 0. There were 2 competing recapture structures, $\{p_{PL}\}$ and $\{p_t\}$. Structure $\{p_{PL}\}$ suggested that recapture rates varied by field supervisor whereas structure $\{p_t\}$ suggested that recapture rates varied with no consistent pattern over time. However, both these competing models contained slope parameters that were not estimated because the real parameter estimates approached 1.0. Therefore, we retained structure $\{p_{t+t^2}\}$ for modeling apparent survival. We examined both an age (a2) and a sex effect before modeling habitat covariates. Neither effect was supported by the data based on AICc rank (i.e., not competing) and slope parameter confidence intervals that included 0; therefore, we did not include these effects in subsequent habitat models.

We examined 10 *a priori* hypothesized models relating the effects of habitat covariates to spotted owl survival (Table 2). The 95% confidence set contained 10 models (Table 8). The top ranked model had an AICc weight of 0.148, and there were 9 competing models (i.e., within 2 AIC_c units); thus, model uncertainty was high. The most parsimonious model, $\{\phi_{MATFOR}, p_{t+t^2}\}$, indicated a positive relationship between the area of mature forest in a territory and spotted owl survival. The direction of this relationship agreed with our prediction (Table 2), but the confidence interval for the habitat slope parameter slightly

overlapped 0 ($_{MATFOR}$ = 0.0049, SE = 0.0029, 95% CI = -0.0007, 0.0106), suggesting the relationship was not strong. MATFOR was highly correlated (r = 0.68 - 0.93, $P < 0.0001$) with covariates in 5 competing models (SOEDG, MATMCFOR, SOCOR, SOMP, and MCFOR), which contributed to model uncertainty in this analysis. Though most of the habitat covariates in the models of the 95% confidence set affected survival as we predicted, the 95% confidence intervals for all slope parameters associated with the covariates included 0. The habitat covariate in the top ranked model, $\{\phi_{MATFOR}, p_{t+t^2}\}$, explained only about 9% of $^2_{spatial}$ in survival, and variation due to sampling error was relatively low (Table 9). The coefficient of spatial process variation for ϕ suggested relatively high variation in survival among territories (Table 9). Based on model $\{\phi_{MATFOR}, p_{t+t^2}\}$, we calculated the mean annual apparent survival within individual territories to be 0.668 (SE = 0.044; range: 0, 1).

Effects of habitat on owl reproductive output in Arizona.—For this analysis, we used the same data that we used in the analysis of climate effects on reproductive output. Thus, we used a compound symmetric covariance structure, and we modeled all habitat covariates with the a2 age structure (i.e., female owls ≥3 years old had a different reproductive output than female owls <3 years old). We examined 10 hypothesized habitat models (Table 2). The resulting 95% confidence set of models contained 8 of the habitat models and the age effect only model (Table 8). The best approximating model, $\{R_{a2+PPOFOR}\}$, indicated that females ≥3 years old fledged more young than females <3 years old and reproductive

output increased with larger areas (ha) of pine and pine-oak forests in the owl territory (Fig. 9). This model was 2.3 times more likely than the second ranked model. The form of this model was

$$R = -0.0401 + 0.5734a2 + 0.0019PPOFOR$$

where a2 was a dummy variable (1 for females ≥3 years old, 0 for females <3 years old), PPOFOR was the area (ha) of pine and pine-oak forest in the territory, $SE_{(0)} = 0.3049$, $SE_{(a2)} = 0.1498$ (95% CI = 0.2782, 0.8687), and $SE_{(PPOFOR)} = 0.0007$ (95% CI = 0.0004, 0.0034). The confidence intervals for both slope parameters excluded 0. The covariate PPOFOR was highly correlated (r = -0.68 to -0.92, $P < 0.0001$) with MATMCFOR, MCFOR, and SOCOR, all of which were effects in other models of the 95% confidence set. The habitat covariate in the most parsimonious model, $\{R_{a2+PPOFOR}\}$, explained 100% of $^2_{spatial}$ in reproductive output; however, there was relatively little spatial variation to be explained because sampling error accounted for about 92% of the total variation in reproductive output (Table 9). Based on the coefficient of spatial process variation, reproductive output varied relatively little among territories (Table 9).

There was 1 competing model, $\{R_{a2+MCFOR}\}$, which indicated that reproductive output decreased ($_{MCFOR} = -0.0015$, SE = 0.0007, 95% CI = -0.0030, -4.6^{E-05}) with increasing area of mixed conifer forest (all seral stages combined) in owl territories. However, based on the spotted owl literature, we made 2 opposing predictions regarding the effect of this habitat covariate on reproductive output.

Population Dynamics of Spotted Owls in New Mexico

Field effort in New Mexico.—During 12 years of study, we conducted 10,045 hours of surveys and located 47 unique spotted owl territories. We located owls in 32 (68%) of these territories in 1994, the year of highest occupancy, but only 16 (34%) territories were occupied in 2001, the year of lowest occupancy (median across all years = 22 occupied territories). We banded 110 territorial owls (including 14 owls that we originally banded as juveniles) and 151 juveniles. The age structure of the population was relatively stable and, in most years, males and females were evenly represented in each age class (Fig. 3). On average, 83.7% (SE = 2.8; range = 67.9, 100) of territory holders were adults (i.e., ≥3 years old) in any given year; the percentage of subadults in the territorial population ranged from 0% in 1997 to 25.6% in 2000 (= 12.0%; SE = 2.6; Fig. 3). On average, 60.1% (SE = 10.55, range = 10.0, 100.0) of owl pairs nested in a year and, of those, 65.8% fledged young (SE = 10.82, range = 0.0, 100.0). The percentage of pairs that fledged 0, 1, 2, or 3 young varied annually (Fig. 4). We recorded complete reproductive failures in 2000 and 2001 (Fig. 4).

Effects of climate on owl survival in New Mexico.—We estimated apparent survival and recapture rates from the capture histories of 110 territorial owls (56 females, 54 males) banded from 1991-2001. The global model fit the data well (χ^2 = 19.1; 38df, P = 0.99) and overdispersion of the data was not evident (χ^2/df = 0.50). The best structure for recapture rates, $\{p_t\}$ (AIC_c weight = 0.950), indicated that recapture rates varied annually without a consistent pattern. There were no competing recapture structures. Annual estimates of p

ranged from 0.712 to 0.975 (= 0.916, SE = 0.0254). The confidence interval for 1 of the 11 parameter estimates (*p* intercept) included 0. We maintained this recapture rate structure in our subsequent survival analyses.

We initially examined 8 models representing the effects of sex, age, and time variation on spotted owl survival. Our best model $\{\phi_{a2}, p_t\}$ indicated that subadult survival (= 0.699, SE = 0.0686, 95% CI = 0.551, 0.815) was lower than adult survival (= 0.859, SE = 0.0186, 95% CI = 0.819, 0.892) for owls in New Mexico. Model $\{\phi_{a2}, p_t\}$ was 8.3 times more likely than the nearest model, and had an AIC_c weight of 0.798. There were no competing models. Though the data supported an age effect in survival, we did not include the a2 effect in the climate models because we did not locate any subadult owls on the study area during 1997. Thus, the effect of climate covariates on subadult survival was unknown during that year.

We next considered 11 hypothesized models relating the effects of climate to spotted owl survival (Table 1). The resulting 95% confidence set included 14 models (Table 10). Model $\{\phi_{a2}, p_t\}$ remained the most parsimonious model based on AIC_c rank (Table 10). There were no competing models. The highest ranking climate model, $\{\phi_{PM}, p_t\}$, was 8.3 times less likely than the top model and indicated that owl survival was positively affected by the number of days of measurable precipitation during the monsoon season prior to the survival interval. However, the confidence interval for the slope parameter associated with P_M included 0 ($_{PM}$ = 0.0506, SE = 0.0368, 95% CI = -0.0216, 0.1227), suggesting the

relationship between survival and monsoon precipitation was weak. The weakness of this relationship was supported by the fact that the climate covariate P_M explained none of ^{2} temporal in survival rates (Table 5). Based on the coefficient of process variation, survival varied little from year to year, and sampling variation accounted for 60% of the total variation in survival (Table 5).

Although most of the climate effects in the competing models within this analysis followed our *a priori* predictions (Table 1), the confidence intervals for all slope parameters associated with climate covariates included 0. In addition, five climate covariates ($P_{W'}$, $P_{\ln W'}$, P_Y, $P_{\ln Y}$, and ZNDX) were highly correlated (r = 0.81-0.99, df = 9, $P \leq 0.004$), which contributed to model uncertainty in this analysis. Thus, our ability to use this set of models to draw inferences regarding the effect of climate on spotted owl survival was limited.

Effects of climate on owl reproductive output in New Mexico.—Annual reproductive output was highly variable, ranging from 0 to 1.81 fledged young per pair (= 0.73), and was based on 10-25 pairs/yr (total 198 pairs over 11 years in 39 territories). The v-c (variance-covariance) structure best supported by the data was compound symmetric; thus, we retained this structure for all reproductive output models. The compound symmetric structure suggested that variance in R was constant among years and covariances between years were also constant.

We first examined 5 hypothesized models for effects of age and time variation on reproductive output (R). Our best model, $\{R_{\text{female a2}}\}$, indicated that reproductive output

was greater for adult (≥3 years old) female owls (= 0.79, SE = 0.191) than for subadult (<3 years old) female owls (= 0.27, SE = 0.227). There were no competing models (AIC_c weight of model $\{R_{female\ a2}\}$ = 0.975). Though the data supported a female age effect on reproductive output, we did not include the a2 effect in the climate models because we did not locate any subadult female owls on the study area during 1997. Thus, the effects of climate covariates on reproductive output of subadult females was unknown during 1997.

We then examined 13 hypothesized climate models (Table 1). Model $\{R_{female\ a2}\}$ remained the best model based on AIC_c rank, and there were no competing models (Table 10). The best climate model, $\{R_{P_{ln\ Y}}\}$, was about 95 times less likely than the top model and indicated that reproductive output was positively affected (in a pseudothreshold relationship) by the number of days with measurable precipitation during the past year. However, the confidence interval for the slope parameter associated with $P_{ln\ Y}$ included 0 ($P_{ln\ Y}$ = 1.2644, SE = 0.8356, 95% CI = -0.6210, 3.1498). The climate covariates in the models of the 95% confidence set (i.e., covariates $P_{ln\ Y}$, ZNDX, and P_Y) were correlated at 0.90-0.99 (df = 10, $P \leq 0.0002$). This correlation was not surprising given that most of the annual precipitation on the New Mexico site fell from June–September (Fig. 2), a period encompassed by the ZNDX (moisture condition) covariate. Together, the models that included these covariates suggested that reproductive output may increase with more precipitation during the 9-20 months prior to young fledging. However, the relative

importance (i.e., sum of AIC_c weights) of these climate effects combined was only 0.027. Reproductive output was highly variable from year to year based on the coefficient of temporal process variation (Table 5). The number of days of measurable precipitation during the past year (i.e., the best climate model) explained about 12% of $^2_{temporal}$ in reproductive output; sampling variation accounted for about 13% of the total variation in R (Table 5).

Model validation using 2002 reproductive output in New Mexico.—In 2002, we surveyed all the territories (n = 16) occupied in 2001. We estimated the reproductive output at all but 1 sampled territory; therefore, we used 15 territories to compare the accuracy of the reproductive output estimate predicted by our modeling described above. Based on the weighted average of our *a priori* climate models, we predicted that 2002 owl reproductive output (R) in New Mexico would be 0.72 fledged young per pair (Table 6). We estimated the empirical reproductive output to be 0.63 fledged young per pair. Thus, our models correctly predicted a moderate R for New Mexico, and the observed value fell within the range of predicted R estimates from the climate models (range = 0.37 - 0.92). In addition, though the average predicted reproductive output value based on the 95% confidence set of models for the 1991-2001 data was very close to the observed empirical value, the predicted value using only the top model (R = 0.82) was higher than the observed 2002 reproductive output.

Effects of climate on owl recruitment in New Mexico.—Because the model structure we used to estimate recruitment rates (f) did not allow for age effects, we used model $\{\phi_{PM}, p_t$

} (i.e., the best survival model without an age effect) as a foundation for this analysis. The global model fit the data ($\chi^2 = 25.61$; 32df; $P = 0.78$) and the data were not overdispersed ($\chi^2/df = 0.80$). Based on a model with no time constraints on recruitment (i.e., model $\{\phi_t, p_t, f_t\}$), we calculated mean annual recruitment during 1993-2001 to be 0.089 (SE = 0.0346; 95% CI = 0.021, 0.157) new territorial owls in year t per territorial owl in year t-1.

After examining 7 hypothesized models that represented the effects of sex and time variation on recruitment rates, the 95% confidence set included 4 models, all of which were competing. The most parsimonious model, $\{\phi_{PM}, p_t, f_{t+t^2}\}$ (AIC_c weight = 0.362), indicated a quadratic trend in recruitment over time, with the lowest recruitment occurring during the interval 1996-1997 (Fig. 10a). The slope parameter estimates for the quadratic trend were precise ($_t = -1.0219$, SE = 0.2054; $_{t^2} = 0.0900$, SE = 0.0192), and the confidence intervals excluded 0 ($_t$ 95% CI = -1.4244, -0.6194; $_{t^2}$ 95% CI = 0.0525, 0.1276); thus, the quadratic trend was supported by the data. A competing model, $\{\phi_{PM}, p_t, f_{s+t+t^2}\}$, which had a sex effect in addition to the quadratic trend, was slightly less likely (AIC_c weight = 0.332) than the top model. This model suggested that annual recruitment was higher for female owls than for male owls. The other 2 competing models, $\{\phi_{PM}, p_t, f_t\}$ and $\{\phi_{PM}, p_t, f_{s+t}\}$, suggested that recruitment rates varied in no consistent pattern over time, either with or without an additive sex effect. The slope parameters for the sex effects in models $\{\phi_{PM}, p_t, f_{s+t+t^2}\}$ and $\{\phi_{PM}, p_t, f_{s+t}\}$ had confidence intervals that included 0; thus,

differences in annual recruitment rates between the sexes were only weakly supported by the data. For this reason, and because the top model did not include a sex effect, we did not include a sex effect in the climate models. In all 4 of the above recruitment models, we fixed the value of 1 recapture parameter (1991) to 1.0 because the value was near 1.0 and was not estimated by Program MARK.

We next examined an additional 7 models representing hypothesized relationships between climate and annual recruitment rates (Table 1). The resulting 95% confidence set was identical to the set described above (i.e., before inclusion of the climate covariates; Table 10). Thus, model $\{\phi_{PM}, p_t, f_{t+t^2}\}$ best explained the data. The highest ranking climate model (AIC_c weight = 0.001) was $\{\phi_{PM}, p_t, f_{ZNDX}\}$, which indicated that wet conditions during March–September of the previous year had a positive effect on spotted owl recruitment (Fig. 10b). Model $\{\phi_{PW'}, p_t, f_{ZNDX}\}$ explained variation in recruitment as

$$\hat{f} = \frac{1}{1 + \exp[-(-2.2931 + 0.3155ZNDX)]}$$

where ZNDX was the average monthly moisture index during March–September of the previous year, $SE_{(0)} = 0.1932$, and $SE_{(ZNDX)} = 0.1306$ (95% CI = 0.0596, 0.5714). The confidence interval for the slope parameter associated with the moisture index did not include 0, suggesting that the relationship between wet conditions and annual recruitment was supported by the data. Based on model $\{\phi_{PW'}, p_t, f_{ZNDX}\}$, moisture conditions

during March–September explained about 84% of $^2_{temporal}$ in annual recruitment rates (Table 5). Sampling error accounted for about 25% of the total annual variation in recruitment, and the coefficient of temporal process variation indicated that recruitment varied widely from year to year (Table 5).

Population rate of change in New Mexico.—Because model $\{\phi_t, p_t, \lambda_t\}$ failed to achieve numerical convergence, we used model averaged estimates of annual apparent survival (ϕ) and recruitment (f) to derive annual estimates of population rate of change (λ) for spotted owls in New Mexico. We used only the models in the 95% confidence set of the recruitment analysis (Table 10) for model averaging. We calculated annual λ using the equation $\lambda_i = \phi_i + f_i$., where i indicated individual years. Derived λ_i ranged from 0.869 to 1.033. Mean λ from 1993-2000 (i.e., the years for which we could estimate λ_i) was 0.937 (SE = 0.0214, 95% CI = 0.895, 0.979). Thus, the spotted owl population was declining at an annual rate of about 6.3%. Based on estimates of realized change (Δ_t), we calculated that 60.8% of the 1993 spotted owl population remained in 2000 (Fig. 8b).

Effects of habitat on owl survival in New Mexico.—We banded 110 spotted owls in 45 territories (including 4 wildfire-altered territories). Of these banded owls, 82 occupied 1 territory during the period that they were under observation, 16 occupied 2 territories, and 12 occupied 3 territories (including 3 owls that occupied 1 territory during non-consecutive years, and occupied a second territory for ≥1 intervening year). The global model fit the data (χ^2 = 13.73, 28df, P = 0.99) and data overdispersion was not evident (χ^2/df = 0.49).

Recapture rates were approximated best by structure $\{p_{lt}\}$, which indicated a declining linear trend in recapture rates over time. The 95% confidence interval for the slope parameter associated with the linear trend excluded 0. We examined both an age (a2) and a sex effect before modeling habitat covariates. The age effect was supported by the data whereas the sex effect was not. Thus, we retained only the a2 structure in all subsequent habitat models. This a2 effect indicated that adult (≥3 years old) owls had higher annual apparent survival than subadult (<3 years old) owls.

We evaluated 10 models representing hypothesized relationships between habitat covariates and spotted owl apparent survival (Table 2). The resulting 95% confidence set contained all 10 of these models in addition to the age effect only model (Table 11). Model uncertainty was moderate. The most parsimonious model, $\{\phi_{a2+SOEDG+SOMP+SOCOR}, p_{lt}\}$, indicated that survival of spotted owls in New Mexico was greater for adults than subadults and, within each age class, increased with (1) increasing edge length between spotted owl habitat and other habitats, (2) larger maximum patch size of spotted owl habitat, and (3) less total core area of spotted owl habitat within the territory. This model was 2.4 times more likely than the second ranked model. Model $\{\phi_{a2+SOEDG+SOMP+SOCOR}, p_{lt}\}$ explained variation in owl survival as

$$\hat{\phi} = \frac{1}{1 + \exp[-(1.7629 + 0.8268a2 + 0.0006SOEDG + 0.0228SOMP - 0.0281SOCOR)]}$$

where a2 was a dummy variable (1 for females ≥3 years old, 0 for females <3 years old),

SOEDG was edge length (km) between spotted owl habitat and other habitats, SOMP was maximum patch size (ha) of spotted owl habitat, SOCOR was total core area (ha) of spotted owl habitat, $SE_{(0)} = 0.4294$, $SE_{(a2)} = 0.3907$ (95% CI = 0.0610, 1.5927), $SE_{(SOEDG)} = 0.0262$ (95% CI = -0.0508, 0.0521), $SE_{(SOMP)} = 0.0093$ (95% CI = 0.0046, 0.0410), and $SE_{(SOCOR)} = 0.0104$ (95% CI = -0.0484, -0.0077). The confidence interval for the SOEDG slope parameter included 0. The confidence intervals for the a2, SOMP, and SOCOR slope parameters in the top model did not include 0, suggesting that the data supported variation in survival due to age class, maximum patch size, and total core area (Fig. 11). The estimated relationship between SOMP and survival agreed with our *a priori* hypothesis whereas the relationship between SOCOR and survival was opposite of our prediction (Table 2). The covariates SOMP and SOCOR were correlated ($r = 0.98$, $P < 0.0001$). The habitat covariates in model $\{\phi_{a2+SOEDG+SOMP+SOCOR}, p_{lt}\}$ explained about 27% of $^2_{spatial}$ in survival; sampling error accounted for about 22% of the total variation in survival (Table 9). Mean survival within individual territories was 0.680 (SE = 0.048; range: 0, 1), but variation in survival among territories was relatively high based on the coefficient of spatial process variation (Table 9).

There were 2 competing models (Table 11). Model $\{\phi_{a2+MATMCFOR}, p_{lt}\}$ contained the same age effect as the top model and suggested that spotted owl survival decreased with increasing area (ha) of mature mixed conifer forest within an owl territory. However, the effect of mature mixed conifer forest was unclear because the confidence interval of the

slope parameter included 0 ($_{MATMCFOR}$ = -0.0045, SE = 0.0030, 95% CI = -0.0104, 0.0013). MATMCFOR was highly correlated with SOMP (r = 0.85, $P < 0.0001$) and SOCOR (r = 0.89, $P < 0.0001$), both covariates in the top model. The final competing model, $\{\phi_{a2}, p_{lt}\}$, did not contain any habitat covariates, but explained variation in survival on territories based on owl age class alone. The habitat covariates in all of the models of this 95% confidence set were highly correlated (r = -0.74 to -0.79 and 0.65 to 0.99, $P <$ 0.0001). However, with the exception of 2 covariates in the top model, all confidence intervals for the habitat slope parameters included 0.

Effects of habitat on owl reproductive output in New Mexico.—We used the same data for this analysis that we used in the analysis of climate effects on reproductive output. Thus, we used a compound symmetric covariance structure, and we modeled all habitat covariates with the a2 age structure (i.e., owls ≥3 years old had a different mean reproductive output than owls <3 years old). The 95% confidence set contained an age effects only model and 9 of the 10 hypothesized models that we examined for the effects of habitat on reproductive output (Table 11). Model uncertainty was high based on the relatively equal AIC_c weights for all models and the fact that all models were within 2 AIC

$_c$ units of the top model. In addition, the confidence intervals for the slope parameters associated with the habitat covariates in all models included 0. The most parsimonious model, $\{R_{a2}\}$, indicated that adult females fledged more young than subadult females (adult: = 0.83, SE = 0.074; subadult: = 0.34, SE = 0.124). The confidence interval for the

a2 slope parameter excluded 0 ($_{a2}$ = 0.5173, SE = 0.1492, 95% CI = 0.2229, 0.8117), which supported a difference in reproductive output between age classes. The best habitat model, $\{R_{a2+OTHER}\}$, suggested that adult females fledged more young than subadult females and reproductive output decreased with larger areas (ha) of OTHER habitat in owl territories. We defined OTHER habitat as any vegetation class in which we did not locate a spotted owl nest or roost tree (*sensu* Franklin et al. 2000). For New Mexico, OTHER habitat was composed of stands of pure aspen forest, piñon-juniper woodland, or grassland. While the predicted effect of OTHER habitat ($_{OTHER}$ = -0.0015, SE = 0.0012) on reproductive output was opposite of our *a priori* prediction (Table 2), the 95% confidence interval for this effect included 0 (95% CI = -0.0039, 0.0009). The covariate OTHER was not highly correlated with any other habitat covariates. In model $\{R_{a2+OTHER}\}$, OTHER accounted for about 4% of $^2_{spatial}$ in reproductive output (Table 9). Sampling error was relatively high, accounting for about 60% of the total spatial variation (Table 9). Based on the coefficient of spatial process variation, reproductive output showed moderate variability among territories (Table 9).

The habitat covariates in the models ranked 3-6 (i.e., SOMP, MATFOR, SOCOR, and MATMCFOR) were highly correlated (r = 0.84 - 0.98, $P < 0.0001$), which likely contributed to model uncertainty. Our *a priori* predictions for the effects of these 4 covariates on reproductive output were correct (Table 2), but the 95% confidence intervals for these effects included 0. Given the high model uncertainty of this model set and the

lack of support (i.e., confidence intervals including 0) for the habitat effects in these models, we believed an age effect only model was the most appropriate model for making inferences.

DISCUSSION

Recent genetic studies suggest that the Mexican spotted owl has been isolated from the 2 coastal subspecies for tens of thousands of years (Barrowclough et al. 1999). During this period of isolation, the Mexican subspecies has been subjected to selection pressures that are different from the coastal subspecies, particularly with respect to annual variation in climate and some physiographic conditions (e.g., canyon habitats). Despite these selection pressures, the Mexican spotted owl appears to exhibit a "bet-hedging" life history strategy similar to the coastal subspecies (Franklin et al. 2000, Seamans et al. 2001, LaHaye et al. *In Review*). This strategy is characterized by high survival, which has low annual variation, and highly variable annual reproduction (Stearns 1976). Under conditions of high environmental stochasticity, such a strategy may be an adaptation that allows an animal to reproduce when conditions are favorable, yet survive unfavorable conditions with little or no reproduction (Sæther et al. 1996). These are the conditions that are typical of spotted owl habitats in the southwestern United States.

We suspect that environmental variability is much greater in the range of the Mexican spotted owl than in the range occupied by the northern and California spotted owls. The occurrence of a seasonal monsoon in the American Southwest is a major climatic feature not occurring on the western coast of the United States. Since 1700, areas within the range

of the Mexican subspecies have been subjected to severe or extreme drought conditions twice as often as areas within the ranges of the 2 coastal subspecies (Cook et al. 1999). Thus, moisture is more likely to be limiting within the range of the Mexican subspecies. In addition, the latitudinal range of the Mexican spotted owl spans temperature to subtropical latitudes, and its range is 2-3 times greater in extent than either of the coastal subspecies. Finally, the physiography within this extensive range is characterized by a variety of disjunct deep canyons, high plateaus, and isolated mountain ranges (Orme 2002). Within this physiographic landscape, the Mexican spotted owl inhabits a diverse array of habitats, including mixed conifer forest, pine-oak forest, and steep-walled rock canyons with little vegetation (Ward et al. 1995). Mexican spotted owl subpopulations are separated by habitats, such as grasslands, shrub-steppes, and deserts, which do not provide conditions for breeding (Block et al. 1995). In contrast, the northern and California spotted owls have relatively contiguous distributions within remaining habitat along major north-south mountain ranges from central California to southern British Columbia, Canada (Gutiérrez et al. 1995). However, the distribution of California spotted owls in southern California resembles the disjunct distribution of the Mexican spotted owl (Noon and McKelvey 1992, LaHaye et al. 1994). Thus, we expect *a priori* that the population dynamics of Mexican spotted owls could be different than the coastal subspecies.

In general, the 2 populations of Mexican spotted owls that we studied had similar vital rates. The estimated spatial and temporal process variation in vital rates were also similar between study areas, but process variation was generally higher than reported for the

northern (Franklin et al. 2000) or California spotted owl (LaHaye et al. *In Review*). Based on coefficients of process variation, both temporal and spatial variation in vital rates were 2-5 greater in the Mexican spotted owl populations we studied than in a population of northern spotted owls (Franklin et al. 2000). Climate and habitat explained relatively little of the temporal and spatial process variation, respectively, in most population parameters that we examined (see details below). In contrast, Franklin et al. (2000) found that climate explained all of the temporal process variation in vital rates of a northern spotted owl population, and habitat conditions explained most of the spatial process variation in vital rates of the same population. LaHaye et al. (*In Review*) found that climate accounted for 100% of the temporal process variation in reproduction of a California spotted owl population, though they did not find any temporal process variation in survival. Our finding of greater variation in the vital rates of the Mexican spotted owl compared to the coastal spotted owl subspecies was consistent with the Mexican spotted owl evolving in a more variable environment. Thus, it was not surprising that relatively simple climate and habitat models had low explanatory power. While some of our models did not provide strong correlations between vital rates and climate and habitat covariates, our results should serve as a base for future research questions and modeling of Mexican spotted owl population dynamics.

Climate and Temporal Variation in Population Parameters

The relative temporal variability in spotted owl population parameters was similar between the populations we studied. Annual survival varied the least over time while

reproductive output and recruitment showed high annual variation. An index of moisture condition provided the best climatic explanation of temporal variation in most vital rates on both study areas. Wet conditions during March–September had a positive effect on Mexican spotted owl (1) survival during the following November–March in Arizona, (2) recruitment during the following November–March in both Arizona and New Mexico, and (3) reproductive output during the following breeding season in Arizona. The moisture index explained most of the temporal variation in recruitment, but only low to moderate amounts of the variation in survival and reproduction. The climate models that we examined did not explain any of the variation in annual survival of spotted owls in New Mexico. Annual reproductive output in New Mexico was positively affected by the number of days of measurable precipitation during the previous November–October, but this climate effect explained little of the year-to-year variation in reproduction.

Precipitation appears to influence the vital rates of spotted owls throughout their range (Franklin et al. 2000, North et al. 2000, Seamans et al. 2002, LaHaye et al. *In Review*, this study). However, the effect of precipitation on each subspecies varies depending on the critical life history periods during which precipitation occurs. In general, Mexican spotted owl vital rates appear to be affected by precipitation several months prior to critical time periods (e.g., nesting season, winter survival period; Seamans et al. 2002, this study). Because the Mexican spotted owl inhabits a relatively xeric environment, this pattern suggests an indirect mechanism, perhaps through primary productivity affecting prey population dynamics (e.g., see Jaksic et al. 1997, Ernest et al. 2000). In contrast,

precipitation appears to affect northern and California spotted owls more directly. Franklin et al. (2000) found that both survival and reproduction of northern spotted owls were negatively affected by increased precipitation during the nesting period. They suggested that increased precipitation during the nesting period may reduce foraging efficiency or increase the energetic costs of nesting and roosting owls (i.e., direct effects). The reproduction of California spotted owls is negatively affected by increased precipitation during the nesting season (North et al. 2000) or by the combined effects of precipitation during the nesting season and during previous years (LaHaye et al. *In Review*). In general, others have found a negative correlation between seasonal precipitation and productivity of raptors (e.g., Gargett 1977, Kostrzewa and Kostrzewa 1990, Steenhof et al. 1999).

We found little evidence that temperature was an important factor explaining variation in vital rates of our study populations. Spotted owls are relatively heat intolerant (Ganey et al. 1993, Weathers et al. 2001). However, we doubt the spotted owl population in Arizona was subjected to heat stress because few days (= 1.5) exceeded 32°C each year. In New Mexico, more days (= 14.2) exceeded 32°C each year, causing a potential for heat stress in owls. In addition, the effects of such heat may have been limited by cooler microclimates at spotted owl nest and roost sites, the relatively higher elevations occupied by owls compared to the weather stations we used, behavioral adaptations by owls (Barrows 1981), or a combination of these factors. The lack of an effect by cold temperatures could be explained by the relatively dense plumage of the owl (Barrows 1981), microclimate conditions, and behavioral adaptations.

Survival.—Estimates of mean annual survival for spotted owls in Arizona (= 0.859) and New Mexico (= 0.856) were comparable to those of the northern spotted owl (= 0.844 for 11 populations, Burnham et al. 1996; = 0.882, Franklin et al. 2000) and California spotted owl (= 0.819 for 5 populations, Franklin et al. *In Press*). We did not model juvenile survival because of potential biases related to permanent emigration (Raphael et al. 1996). However, we estimated minimum values based on empirical data. The proportion of owls banded as juveniles in any given year that subsequently became territory holders ranged from 0.00-0.64 (= 0.23, SE = 0.064) in Arizona and from 0.00- 0.27 (= 0.08, SE = 0.028) in New Mexico. This suggested that juvenile survival was quite variable, recruitment was quite variable, annual dispersal patterns varied, or some combination of these factors. Our juvenile survival estimates for Arizona were comparable to estimates for the other 2 subspecies (Burnham et al. 1996, Blakesley et al. 2001, LaHaye et al. 2001). It was not clear whether the much lower estimates for New Mexico reflected a bias due to emigration, or true lower survival rates.

Spotted owl survival in Arizona varied with moisture conditions during March–September prior to the winter stress period; this climate effect explained about half of the temporal process variation. In New Mexico, our climate models did not explain any of the observed temporal process variation in survival rates. The lack of a stronger explanatory relationship between climate and survival in these populations may be due to (1) the absence of a strong climate effect, (2) climate affecting survival through some variable or combination of variables that we did not consider, or (3) a buffering effect by

habitat (Franklin et al. 2000). A buffering effect of habitat seems unlikely given the low (8% Arizona, 27% New Mexico) explanatory power of habitat covariates in our study. Additional years of study or the inclusion of other covariates could provide a better understanding of the relationships among climate, habitat, and survival.

Seamans et al. (2002) found positive relationships between precipitation and survival in the same populations we studied. However, there were some differences between the 2 studies regarding the precipitation covariates that best explained the variation in survival and the amount of temporal variation explained by these covariates. Seamans et al. (2002) did not consider a moisture index, but found that the same amount of variation (53%) in survival of owls in Arizona was due to the previous monsoon season, a period of precipitation that was incorporated into our moisture index. Seamans et al. (2002) found that precipitation during the previous year in New Mexico explained 56% of the temporal variation in survival rates. We found that none of this temporal variation could be accounted for by climate. However, we could not draw strong inferences because our analysis of the effects of climate on survival in New Mexico suffered from high model uncertainty. Thus, additional years of data could result in conclusions contrary to ours. In addition, subsequent to Seamans et al. (2002) study, the populations experienced more dramatic extremes in precipitation, which added considerable variation to the explanatory metrics.

Franklin et al. (2000) found that survival of northern spotted owls was negatively affected by cold, wet spring conditions. We did not assess the effects of spring weather on

Mexican spotted owl survival because on average we identified (captured or resighted) 50% of the territorial owls before 15 May each year. Thus, the sampling period overlapped the spring survival period.

Reproductive output.—Reproductive output fluctuated widely on both study areas. Over the 11 years of study, the mean annual reproductive output estimate for owls in Arizona (= 0.929) was high and the estimate for New Mexico was similar (= 0.702) to an estimate for the northern spotted owl (= 0.613, Franklin et al. 2000). The high variability in reproductive performance of Mexican spotted owls suggested that occasional years of high reproduction followed by good survival conditions for subadult owls may provide a means for rapid recovery following a population decline.

The reproductive output of spotted owls on both study areas appeared to respond to precipitation after a lag time of ≥9 months. Such a lag may be the result of a bottom-up trophic effect (Ernest et al. 2000) which results in an increase in prey abundance. However, many of the climate models that we examined in the analyses of reproductive output performed equally well based on AIC_c ranking. This, in combination with the relatively low proportion of temporal process variation explained by the covariates in the best climate models, suggested that multiple climatic factors may influence annual reproduction in Mexican spotted owls.

Seamans et al. (2002) reported similar lag effects between precipitation and reproduction in these spotted owl populations. They found that 73% of temporal variation in reproductive output in Arizona could be attributed to precipitation during the previous

year, while 42% of temporal variation in reproductive output in New Mexico was attributed to precipitation during the previous monsoon season. We found that 42% of the temporal variation in reproductive output in Arizona was explained by an index reflecting moisture conditions from the previous year. In New Mexico, we found that precipitation during the previous year accounted for 12% of temporal variation in reproductive output. Thus, the amount of explained variation in this parameter decreased by about 30% for each study area with our analysis. The differing results from these 2 analyses were probably due to the additional years ($n = 3$) of data available for our analysis as well as the weather extremes observed during these years (see above).

Reproduction in northern and California spotted owls was negatively affected by precipitation during the nesting period (Zabel et al. 1996, Franklin et al. 2000, North et al. 2000, LaHaye et al. *In Review*) or during the previous fall and winter (Wagner et al. 1996). We found no evidence of such effects on reproduction in Mexican spotted owls. These contradictory results may be explained by differences in annual precipitation patterns within the ranges of the subspecies, where more spring rainfall occurs in west coast environments. LaHaye et al. (*In Review*) also found that reproduction of California spotted owls in a southern California mountain range was positively correlated with precipitation during previous years. This could be viewed as a similarity between California spotted owls in southern California and Mexican spotted owls, both of which occupy drier, more variable habitats.

Recruitment.—Our estimates of recruitment (= 0.145 for Arizona, = 0.089 for New

Mexico) were similar to those reported for the northern spotted owl by Franklin et al. (2000) using similar methods. We found that moisture conditions during the previous March–September provided the best climatic explanation of temporal process variation in annual recruitment rates on both study areas. Recruitment is a function of multiple population parameters, including reproductive output during previous years, juvenile survival, and immigration. Of these, we estimated only reproductive output. In Arizona, we found reproductive output was positively affected by March–September moisture conditions as well, and moisture conditions explained a similar amount of the temporal process variation in reproduction (42% for reproduction, 32% for recruitment). Thus, we hypothesize that most of the effect of March–September moisture conditions in Arizona acts through the reproductive component of recruitment. In New Mexico, reproductive output was positively affected by annual precipitation, though the evidence for such an effect was weak based on the low (12%) proportion of temporal process variation explained by the climate covariate and a covariate confidence interval that included 0. By contrast, March–September moisture conditions in New Mexico explained most (84%) of the temporal process variation in annual recruitment rates and the confidence interval for the covariate slope parameter excluded 0. Therefore, we hypothesize that March–September moisture conditions influenced 1 of the other components of recruitment (i.e., juvenile survival or immigration) for owls in New Mexico.

Habitat and Spatial Variation in Population Parameters

Spatial process variation in survival and reproductive output of spotted owls was

similar, both within and across study areas. However, there was no consistent habitat covariate at the territory scale that explained spatial variation in vital rates. Block et al. (1995) divided the range of the Mexican spotted owl into 11 Recovery Units based on physiographic and biotic features as well as similar landuse histories. Both of our study areas were within the Upper Gila Mountains Recovery Unit. Therefore, if habitat quality was relatively homogeneous throughout the recovery unit, then spatial variation in vital rates would be similar between the study areas.

In general, the habitat covariates in the best approximating models explained <27% of the spatial process variation in Mexican spotted owl survival and reproductive output. The 1 exception occurred in Arizona, where the area of pine and pine-oak forests in owl territories accounted for 100% of the estimated spatial process variation in reproductive output. However, after accounting for sampling error, only 8% of the total variation was spatial process variation that could be attributed to differences in habitat among territories. Thus, after adjusting for sampling error, the area of pine and pine-oak forests in owl territories accounted for 8% of the variation in reproductive output.

There are several possible reasons for the poor explanatory power of habitat covariates in the other analyses of spatial variation that we conducted (i.e., survival in both Arizona and New Mexico and reproduction in New Mexico). First, landscape scale habitat composition and configuration may have little effect on the vital rates we examined. Zimmerman et al. (2003) stated that habitat at the territory scale did not correlate with survival or reproduction in a population of California spotted owls. Ward (2001) found

little evidence that macrohabitat variables affected reproductive output of Mexican spotted owls. Ganey and Dick (1995) suggested that a suitable microclimate may be the primary factor affecting Mexican spotted owl selection of nesting and roosting habitat. Because suitable microclimate conditions occur at spatial scales smaller than individual spotted owl territories (Ting 1998), it is possible that there is not a strong correlation between landscape scale habitat covariates and owl survival or reproduction. Peery et al. (1999) and May and Gutiérrez (2002) found correlations between Mexican spotted owl presence and habitat composition at the landscape scale. However, the habitat selected by Mexican spotted owls in these studies may not have affected owl vital rates in a manner that was detectable by our analyses.

Second, the habitat covariates we examined may not have provided a useful index for the spatial factor that influenced survival and reproduction. For example, the primary prey of Mexican spotted owls on our study areas were Mexican woodrats (*Neotoma mexicana*) and white-footed mice (*Peromyscus* spp.; Seamans and Gutiérrez 1999). Mexican woodrats occurred primarily in rock outcrops and white-footed mice were habitat generalists (Goodwin and Hungerford 1979, Hoffmeister 1986). Rock outcrops were present in all habitat types on our study areas (personal observation). However, we did not estimate the distribution or abundance of rock outcrops because they were concealed by the forest canopy or too small in extent (i.e., they would not have been detected by the Landsat imagery we used for habitat classification). The success of Franklin et al. (2000) in explaining most of the spatial process variation in survival and reproduction of northern

spotted owls may have been due to the dominance of a single prey species in the owl's diet and a relatively well-defined ecotone along which the prey can be found. In addition, logging and other habitat change within the range of the northern spotted owl has resulted in relatively distinct differences (e.g., clearcut edges) in forest structure between managed and unmanaged areas (i.e., unsuitable and suitable habitats). In contrast, within the range of the Mexican spotted owl, clearcut logging has been uncommon, and managed forests are not necessarily obvious without close inspection.

A third possible explanation for the relatively low habitat effect in our study is that factors other than habitat had a greater influence on the spatial variation in owl survival and reproduction. Zimmerman et al. (2003) suggested that spatial variation in the vital rates of a population of California spotted owls was a combination of habitat, variation in the intrinsic survival and reproductive capacities of individual owls, social factors, and stochastic variation among territories. We attempted to account for intrinsic variation of individual owls to some extent by examining support for age effects in the data. We found no support for an age effect in owl survival in Arizona. Although we found evidence for age effects in survival of owls in New Mexico and reproductive output of owls in Arizona, age accounted for none of the spatial process variation in these parameters. Age accounted for 7% of the spatial process variation in owl reproductive output in New Mexico; by contrast, the habitat covariate in the top model accounted for 4% of the spatial variation. Given our data, we could not address the importance of social factors or stochasticity in spatial variation. Nevertheless, the effects of habitat were likely confounded with the

effects of individual owls because very few individual owls occupied more than 1 territory during our study.

Fourth, the results of our habitat models might have been improved by using different remote sensing imagery and different software to develop habitat maps for each study area. We used Landsat 5 Thematic Mapper imagery, IDRISI 4.1 (Eastman 1994) software, and a supervised classification procedure (Lillesand and Kiefer 1994), which resulted in 80% and 77% classification accuracies for the Arizona and New Mexico study areas, respectively. Any given classification technique might be insensitive to subtle vegetation characteristics that could be important to a spotted owl selecting a territory. Therefore, use of a different combination of remote sensing equipment, classification software, and classification procedure might have improved our ability to make inferences regarding the effects of habitat on spotted owl vital rates.

Finally, the explanatory power of habitat covariates might have been improved by reducing sampling variation (i.e., the variation associated with estimating a parameter from sample data). Sampling variation can be reduced by increasing the sample size or improving the study design (e.g., stratification of sampling units). Our study areas were as large as possible given funding levels and the logistical constraints (i.e., multiple visits) related to accurately estimating survival and reproduction in each owl territory. Ideally, an examination of the effect of habitat on vital rates should have included the full spectrum of habitats occupied by Mexican spotted owls. However, this subspecies consists of disjunct populations that inhabit a variety of habitats throughout its range (Ward et al. 1995), and

these habitats vary with latitude and elevation. Therefore, an ideal study design would involve sampling across habitat strata, which necessarily implies sampling different populations. Such a design would be impossible to implement without a great deal of funding.

It is interesting to note that increasing circumstantial evidence suggests that mixed conifer forest may not be optimal habitat for Mexican spotted owls. We found that increasing area of mixed conifer forest of all seral stages was negatively correlated with the reproductive output of owls in Arizona. Though the habitat covariate representing mixed conifer forest was not in the best supported model, it was in the only competing model and the negative effect was supported by the data based on the covariate confidence interval, which did not overlap 0. White et al. (1995) found that mixed conifer forest was negatively correlated with reproduction and persistence of Mexican spotted owls, but they attributed this result to confounding with other variables (e.g., weather, geographic location). Nevertheless, it is possible that geographic differences in vital rates are partially due to habitat, because the relative amounts of vegetation types in owl territories varies by physiographic area (Ganey and Dick 1995). We also found weak evidence that increasing areas of mature mixed conifer forest within owl territories might negatively affect spotted owl survival in New Mexico. Ward and Block (1995) reported that winter prey abundance was lower in mixed conifer forest than in other vegetation types within Mexican spotted owl territories. Owls in New Mexico selected mature mixed conifer forest at the landscape scale when settling on territories (Peery et al. 1999). Thus, prey may be a limiting factor

for owls in New Mexico during the winter stress period.

Population Rate of Change and Relationships Among Estimated Population Parameters

Based on annual estimates of rate of change (λ), both populations experienced wide fluctuations in owl numbers during the course of study. Two lines of evidence suggested these fluctuations were natural and not due to habitat destruction or sampling bias. First, with the exception of the HB Wildfire in New Mexico, which burned 4 owl territories, relatively little habitat change occurred on these study areas as a result of logging or other factors during the study period. Federal listing of the subspecies (USDI 1993) under the Endangered Species Act essentially ended timber harvests on our study sites. Thus, the populations were fluctuating in the absence of habitat alteration. However, a lag effect may have occurred; that is, habitat change due to logging activity before our study began may have affected owl vital rates during subsequent years. Second, the fluctuations likely reflected actual changes in numbers of all owls, both territorial and nonterritorial (i.e., floaters). Subadult territory holders were more common when the populations were stable or increasing than when the populations were declining (Fig. 12). In addition, most owls that we banded as fledglings entered the territorial population within the first 2 years of life (Fig. 13), which suggested that floaters were uncommon.

The population rate of change provides an estimate of the change in numbers of animals from 1 point in time to another; $\lambda>1$ indicates an increasing population whereas $\lambda<1$ indicates a decreasing population. λ integrates information from numerous aspects of a

population, namely the initial population size, survival, reproduction, immigration, and emigration. Each of these components can be subdivided by sex and age class. We estimated 3 parameters that can be associated with λ, survival (ϕ), reproductive output (R), and recruitment (*f*). R is a component of *f*, the other 2 components being juvenile survival and immigration. Survival and recruitment can be related to population rate of change using the simple equation $\lambda = \phi + f$. Using this equation and our estimated mean annual survival (~0.86 for each study area), the minimum recruitment necessary to maintain each population would be 0.14 territorial owls in year *t* for every territorial owl present in year *t*-1. This value closely matches our estimated mean annual recruitment (= 0.145) for the Arizona population, and we found that population to be relatively stable. However, spotted owl recruitment in the New Mexico population was about 0.09, and our estimates of λ indicated the population was declining about 6% per year. In the spotted owl populations we studied, survival was high and varied little over time relative to recruitment. Thus, we expected temporal variation in λ to be affected primarily by recruitment, which varied greatly over time. Franklin et al. (2000, *In Press*) suggested that temporal variation in population rate of change was driven by recruitment in northern and California spotted owl populations as well.

Because the stability of these spotted owl populations was dependent on recruitment and annual variation in this parameter was high, we believe that both populations will continue to fluctuate widely. Increased environmental stochasticity can lead to an increased probability of extinction (Goodman 1987, Shaffer 1987). In addition, low population levels

can cause extinction vortices that result from demographic stochasticity (e.g., inbreeding depression, location of a mate; Gilpin and Soulé 1986). Annual monsoon rainfall was about 70% of normal on both our study areas from 1993 to 1997 (Western Regional Climate Center 2002). During the same period, the number of territorial owls on each study area decreased by about 45%. Thus, long-term drought conditions could reduce population viability. However, given favorable conditions for multiple years, these populations appear capable of rebounding quickly. For example, the Arizona population reached its lowest level (n = 33 owls) in 1997, and then the population increased 76% (n = 58 owls) by 2000 following several years of normal or above normal precipitation. Wide population fluctuations may be common for populations of Mexican spotted owls. Based on genetic evidence, Barrowclough and Groth (1999) suggested that the size of 1 Mexican spotted owl population, which included the owls on our Arizona study site, has been relatively stable for thousands of years. Presumably during this time, extended periods of drought occurred. Because recruitment and reproduction in the New Mexico population were lower and more variable than in the Arizona population, we would expect the New Mexico population to experience more extreme fluctuations in numbers and recover more slowly from a decline.

Management Implications

Though we found moderate levels of spatial variation in survival and reproductive output of the owl populations we studied, we failed to account for this variation using territory scale habitat characteristics. Thus, we conclude that either we did not incorporate

the appropriate covariates into *a priori* models, or the interaction among habitat at the territory scale, climate, and the fitness of individual owls was far more complex than could be depicted by our set of *a priori* hypotheses. If the effects of habitat are to be related to vital rates, then controlled, manipulative experiments of habitat characteristics will be required. Only true experiments can reveal cause and effect relationships (e.g., Platt 1964) and will allow a better understanding of how management decisions can assure the persistence of spotted owls in the Southwest. For example, wildfires on a limited scale probably do not adversely affect spotted owl survival and reproduction (Bond et al. 2002). Under the proper conditions (i.e., experimental design, timing and intensity of fire) prescribed fire may prove useful in the creation or maintenance of habitat for spotted owls or their prey. Experiments should have clearly defined goals and should address a specified aspect of Mexican spotted owl ecology. After an experiment has been initiated, adaptive management (Walters and Holling 1990) techniques should be used to monitor progress toward the specified goals and to make additional habitat management decisions if necessary.

An important area for research is estimation of the relative benefit conferred to spotted owls by different types of habitat (e.g., pine-oak forest compared to mixed conifer forest). Owl territories in New Mexico contained more mixed conifer forest than owl territories in Arizona (Peery et al. 1999, May and Gutiérrez 2002). The density of owls was greater on the New Mexico study area than on the Arizona study area. Owls on both study areas had similar survival rates, but reproductive output was lower for owls in New Mexico.

Therefore, mixed conifer forest may support a higher density of owls while conferring reduced fitness. Research regarding this issue could be conducted in the absence of manipulative management. Such a study would require an experimental design that would account for confounding factors like climate and physiography (e.g., Ganey et al. 2001). If research establishes that fitness varies by habitat type, then additional (or, ideally concurrent) research can evaluate the component(s) of habitat (e.g., primary production, prey populations) responsible for the difference in fitness.

In the absence of experiments, we recommend that habitat management focus on available information regarding the habitat ecology of this species, especially at the microhabitat scale. Natural resource managers should maintain mature, closed canopy forests (i.e., spotted owl habitat); the association between spotted owls and such forests has been documented throughout the range of the Mexican spotted owl (Ganey and Balda 1994, Ganey and Dick 1995, Ganey et al. 1999, Peery et al. 1999, May and Gutiérrez 2002). In addition, managers should assure that sufficient area of forest is being managed to reach target levels to serve as suitable spotted owl microhabitat (Block et al. 1995:91-95) in the future. Our results suggest that Mexican spotted owl reproduction and recruitment may be affected by unpredictable and uncontrollable climate patterns. If this is the case, managers may be limited in their efforts to mediate the large annual fluctuations in these parameters through macrohabitat management. However, survival varied more over space than time. Though we could explain relatively little of the spatial variation in survival, spotted owl population rate of change is most sensitive to changes in adult survival (Noon and Biles

1990, Blakesley et al. 2001, Seamans et al. 2001). Therefore, small gains made in habitat management may increase the persistence of populations.

Our results stressed the importance of acquiring long-term data for long-lived species. Seamans et al. (1999) reported that populations on both of these study areas were declining by ≥10% annually and speculated that owl survival rates in Arizona may have been declining over time. With 4 additional years of data, we were able to conclude that the decline observed by Seamans et al. (1999) on the Arizona study area was temporary, whereas the decline in New Mexico appeared to be continuing. Seamans et al. (2002) reported that climate effects accounted for higher percentages of temporal variation in reproductive output than we found. Since 1998 (the last year included in the analysis of Seamans et al. [2002]), precipitation on both study areas included extremes not observed during 1991-1998. As a result, spotted owls on both study areas experienced extremes, both high and low, in reproductive output. However, precipitation and reproduction did not follow the relationship found by Seamans et al. (2002). For example, monsoon precipitation was above average on both study areas in 1999. This should have produced above average reproduction; instead, owls on both study areas experienced below average reproduction. Inferences made from vital rates of populations are strengthened when the data used in the modeling process includes the full spectrum of variability that might be experienced by study animals. Extremes in weather or habitat conditions (i.e., environmental stochasticity) can cause extreme declines or increases in population size (Goodman 1987, Shaffer 1987). Therefore, effective management of a species requires

information regarding the effect of extreme environmental conditions on vital rates. Such data may be particularly important for the management of the Mexican spotted owl, which inhabits an environment characterized by extreme climate.

Results from this study revealed that the delisting criteria in the Mexican Spotted Owl Recovery Plan (Block et al. 1995) needed to be revised. The delisting criteria were based on the assumptions that Mexican spotted owl populations would not exhibit much temporal variability and that a 20% reduction in territorial owls over 10 years would be cause for concern. However, our study showed that spotted owl populations could experience >20% fluctuations in numbers from year to year. While the Recovery Team is in the process of revising the Plan, including the delisting criteria, our results stress the importance of long-term research. Most recovery plans have been written without sufficient data to address many of the details related to population viability and habitat management (Clark et al. 2002). Thus, successful recovery of listed species and their habitats depends on continuing research and incorporation of techniques such as adaptive management (Walters and Holling 1990).

The data used in the management of natural resources must be based on proper model development and interpretation. Through our model validation results, we demonstrated that a proper modeling procedure, including *a priori* model development, objective model selection, assessment of model uncertainty, and model averaging (Burnham and Anderson 1998) can produce results useful for biological inference. We used 11 years of data to model the effect of climate on spotted owl reproductive output. We then validated the

utility of the resulting model set for each of 2 study areas by accurately estimating spotted owl reproductive output during an additional year of sampling in 2002. Our validation procedure stressed the importance of assessing model uncertainty using AIC_c weights and the need to base inferences on a 95% confidence set of models (Burnham and Anderson 1998). A weighted average (using AIC_c weights) of predicted reproductive output values from the 95% confidence set of climate models provided an accurate estimation of 2002 reproduction on each study area.

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Figure 1. Locations of the Mexican spotted owl study areas in Arizona and New Mexico.

Figure 2. Mean monthly maximum temperature (^{O}C), minimum temperature (^{O}C), and precipitation (cm) on (A) the Arizona study area and (B) the New Mexico study area, 1989-2001.

Figure 3. Percentages, by year, of male (M) and female (F) Mexican spotted owls in 4 age classes (first-year subadult, second-year subadult, adult, and unknown) on 2 study areas in (A) Arizona and (B) New Mexico, 1991-2001.

Figure 4. Percent of Mexican spotted owl pairs that fledged 0, 1, 2, 3, or 4 young each year on study areas in (A) Arizona and (B) New Mexico, 1991-2001.

Figure 5. Relationship of annual apparent survival for Mexican spotted owls from (A) the overall best supported model $\{\phi_t, p_{t+t^2}\}$, which indicated no consistent pattern over time, and (B) the best supported climate model $\{\phi_{ZNDX}, p_{t+t^2}\}$, which indicated a positive linear trend between apparent survival and a moisture index. Modeled data were for Arizona,1991- 2001. The moisture index was calculated by averaging monthly Palmer Z Index (ZNDX) values from March–September for the study area. Positive and negative index values represent conditions wetter and drier than normal, respectively. Point estimates and 95% confidence intervals (error bars) in both graphs were from model $\{\phi_t, p$

$t+t^2\}$. The thick line in (B) was the predicted moisture effect from model $\{\phi_{ZNDX}, p_{t+t^2}\}$.

Figure 6. Relationship between annual reproductive output (R) of female Mexican spotted owls and a moisture index for Arizona, 1991-2001. Point estimates were from observed data. Error bars represent 95% confidence intervals. The line represents the predicted relationship between moisture and R. The moisture index was calculated by averaging monthly Palmer Z Index (ZNDX) values from March–September of each year. Positive and negative index values represent conditions wetter and drier than normal, respectively.

Figure 7. Predicted relationships between Mexican spotted owl annual recruitment and (A) a quadratic trend over time and (B) a linear moisture effect for Arizona, 1993-2000. Point estimates and 95% confidence intervals (error bars) in both graphs show annual recruitment estimates from a model with no constraints on time. We calculated the moisture index by averaging the monthly Palmer Z Index values for March–September of each year. Positive and negative index values represent conditions wetter and drier than normal, respectively.

Figure 8. Estimates of realized rate of change (Δ_t) for Mexican spotted owl populations in (A) Arizona and (B) New Mexico, 1993-2000. Arizona Δ_t were calculated from the best approximating model $\{\phi_t, p_t, \lambda_t\}$, which estimated annual population rate of change (λ) directly from recapture data. New Mexico Δ_t were calculated from λ values derived from

annual survival (ϕ) and recruitment (f) estimates using model $\{\phi_{PW'}, p_t, f_{t+t^2}\}$.

Figure 9. Predicted relationships between reproductive output (R) of female Mexican spotted owls in 2 age classes (≥3 years old and <3 years old) and the area of pine and pine-oak forests in their territories in Arizona, 1991-2001. Predicted values based on the best approximating habitat model $\{R_{a2'+PPOFOR}\}$.

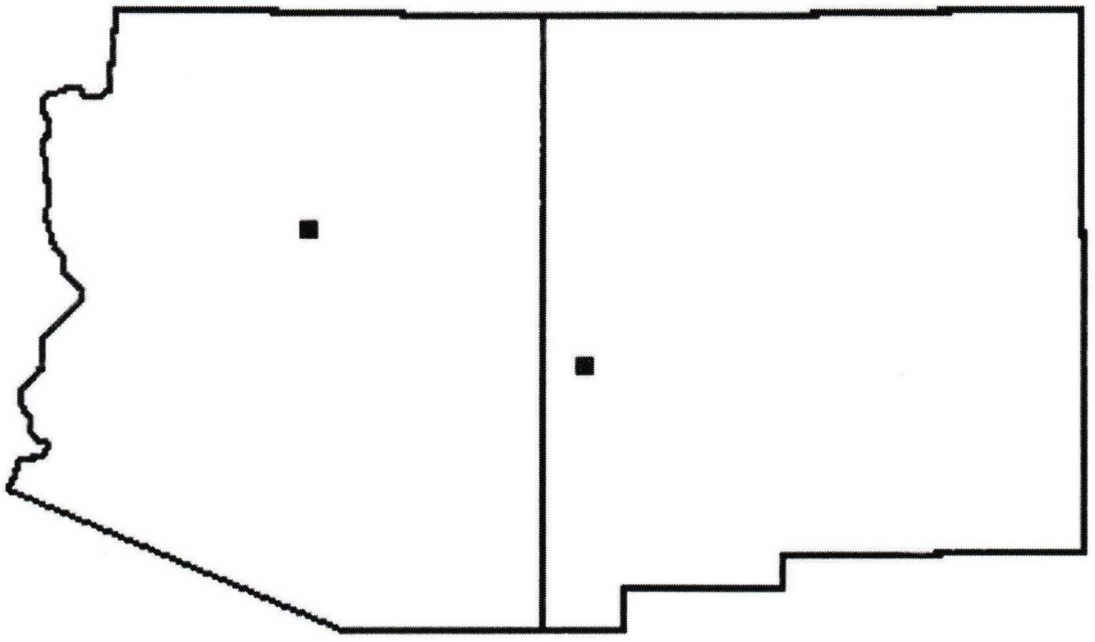
Figure 10. Predicted relationships between Mexican spotted owl annual recruitment and (A) a quadratic trend over time and (B) a linear moisture effect for New Mexico, 1993-2000. Point estimates and 95% confidence intervals (error bars) in both graphs show annual recruitment estimates from a model with no constraints on time. We calculated the moisture index by averaging the monthly Palmer Z Index values for March–September of each year. Positive and negative index values represent conditions wetter and drier than normal, respectively.

Figure 11. Predicted annual survival probabilities of (A) adult (≥3 year old) and (B) subadult (<3 years old) Mexican spotted owls in relation to increasing patch size of spotted owl habitat (SOMP) and decreasing total area of core spotted owl habitat (SOCOR) within territories on the New Mexico study area, 1991-2001. Predicted values based on the best approximating model $\{\phi_{a2+SOEDG+SOMP+SOCOR}, p_{1t}\}$.

Figure 12. Proportion of subadult (≤2 years old) Mexican spotted owls in the territorial

population as the population rate of change varied over time on study areas in (A) Arizona and (B) New Mexico, 1993-1999.

Figure 13. Proportion of fledged young that entered the territorial population of Mexican spotted owls after 1-5 years for study areas in (A) Arizona and (B) New Mexico, 1991-2000.

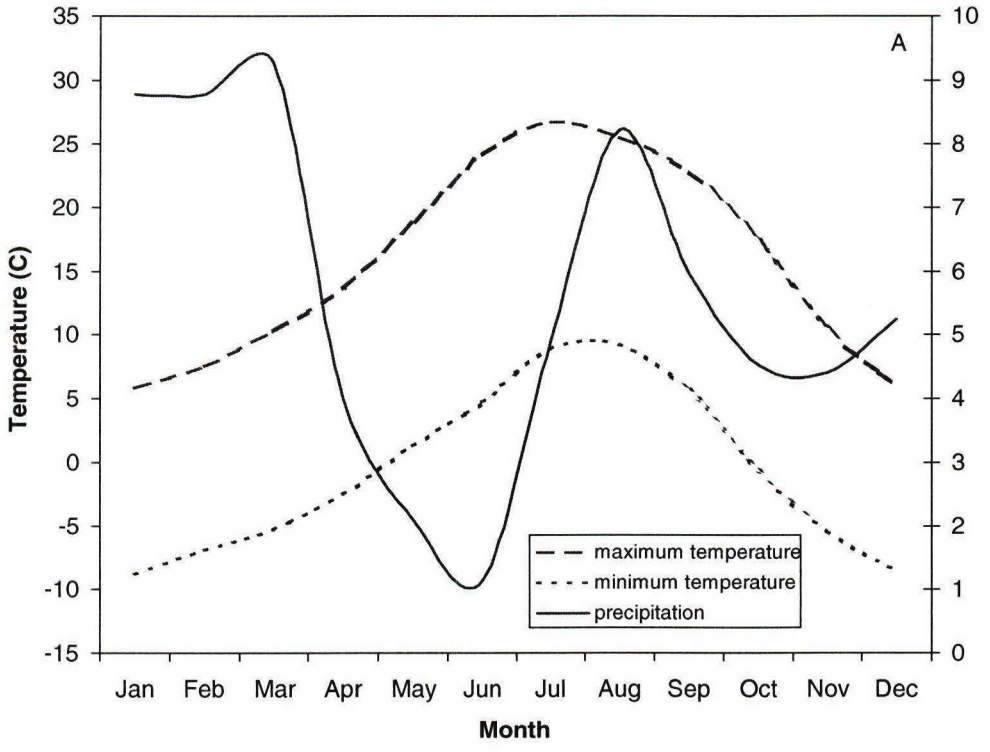


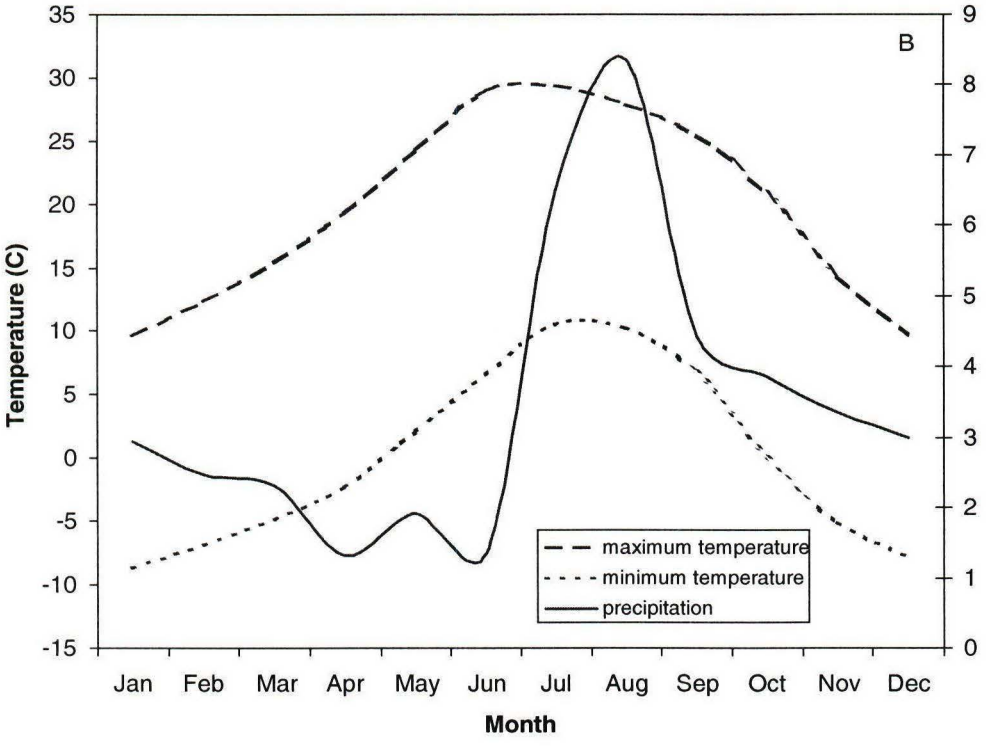
New Mexico

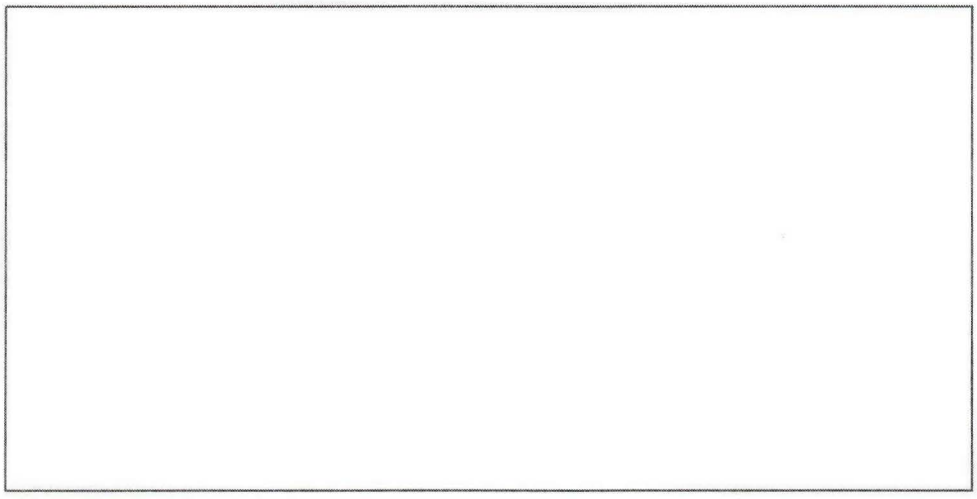
Study Area

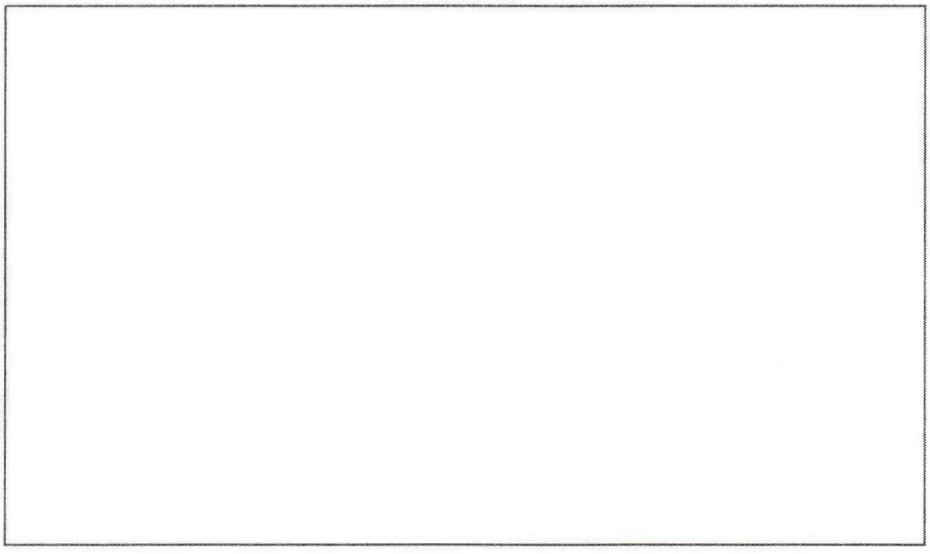
Arizona

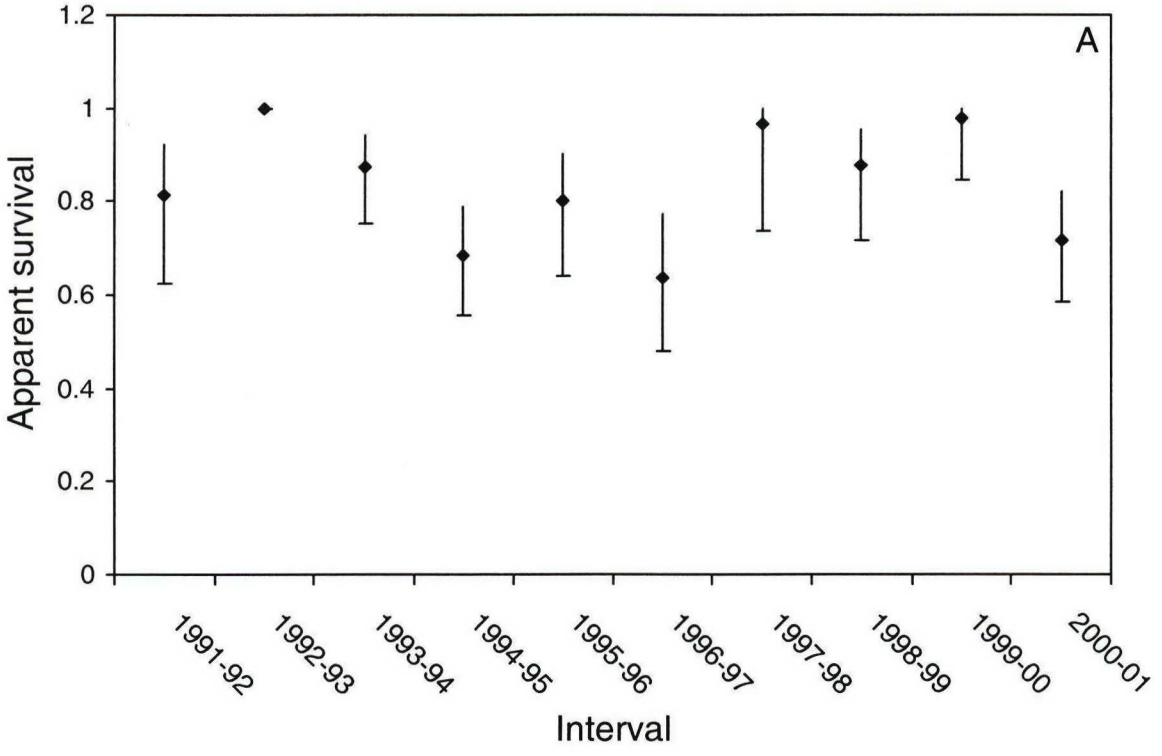
Study Area

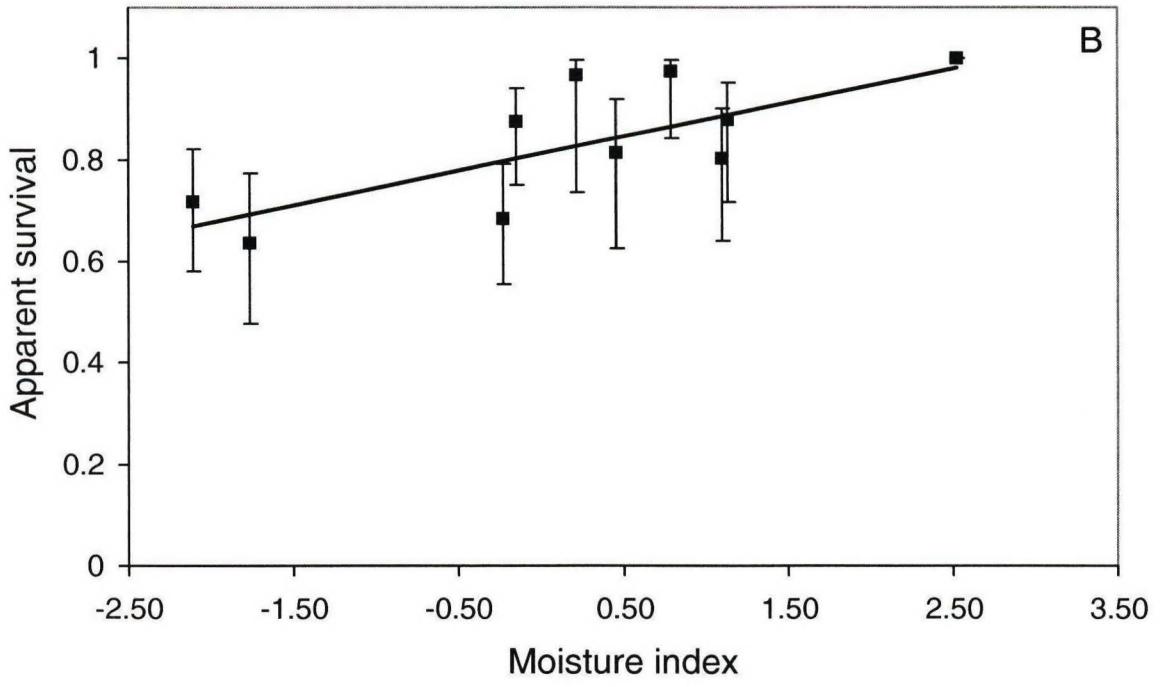

A
Temperature (C)
35
30
25
20
15
10
5
0
-5
-10
-15
10
9
8
7
6
5
4
3
2
1
0
maximum temperature
minimum temperature
precipitation
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
Month

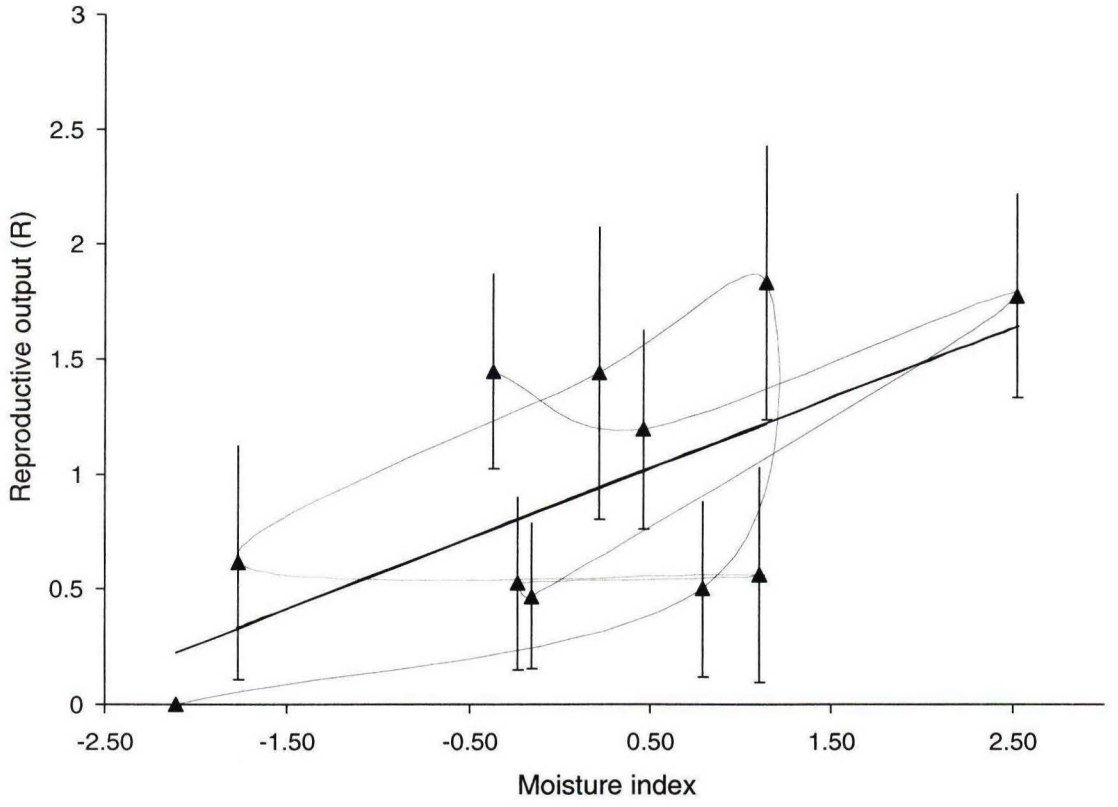

B
Temperature (C)
35
30
25
20
15
10
5
0
-5
-10
-15
9
8
7
6
5
4
3
2
1
0
maximum temperature
minimum temperature
precipitation
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
Month

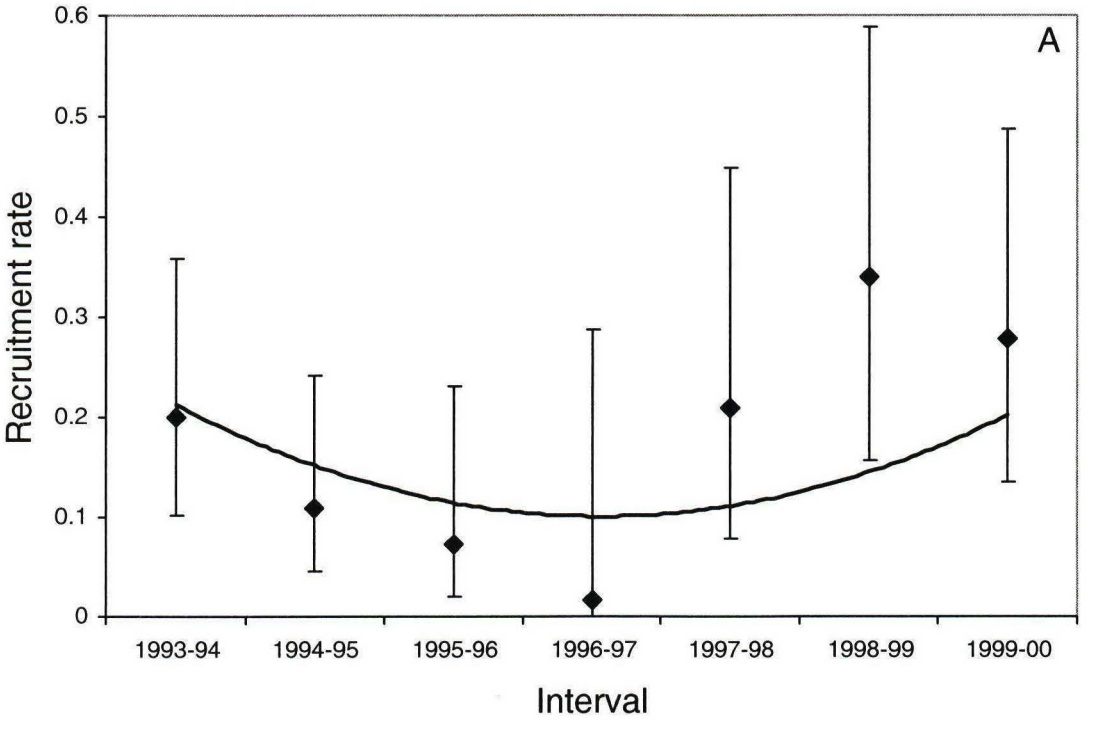


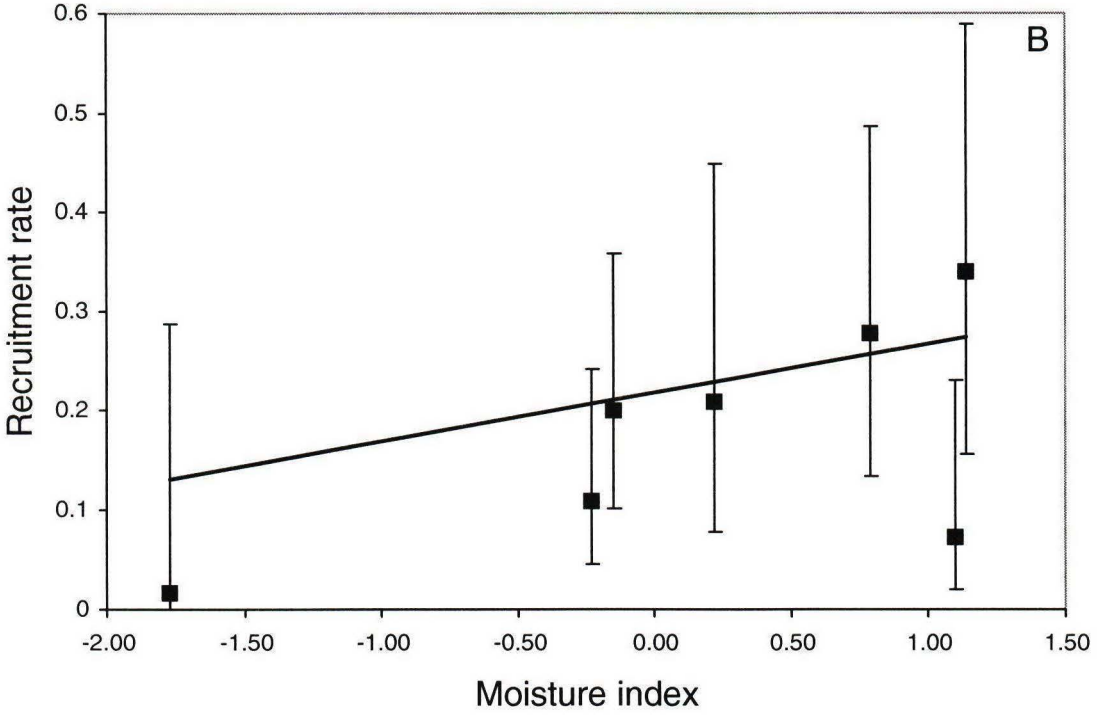


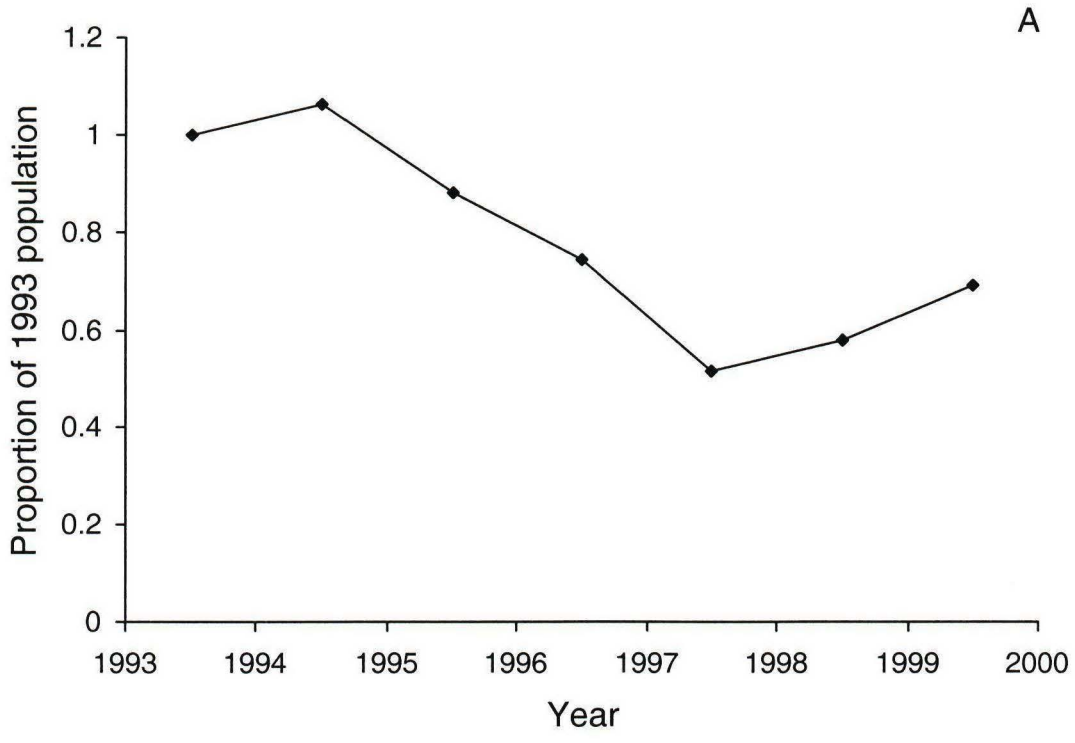

A
Apparent survival
1.2
1
0.8
0.6
0.4
0.2
0
1991-92
1992-93
1993-94
1994-95
1995-96
1996-97
1997-98
1998-99
1999-00
2000-01
Interval

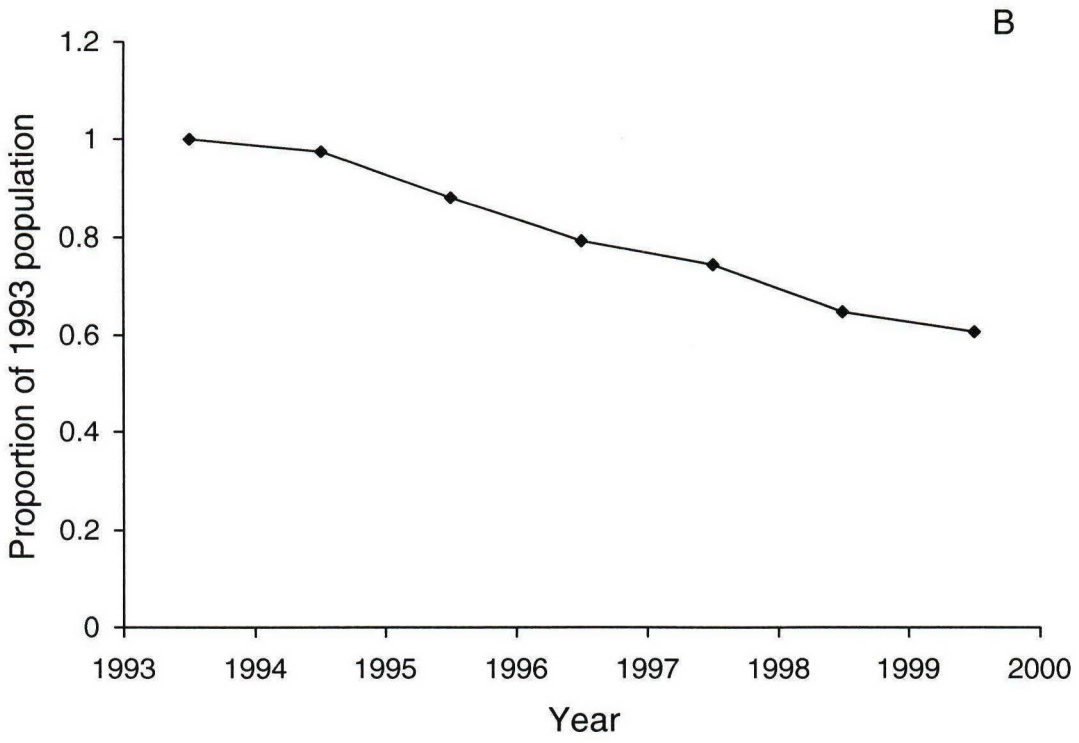

B
Apparent survival
1
0.8
0.6
0.4
0.2
0
-2.50
-1.50
-0.50
0.50
1.50
2.50
3.50
Moisture index

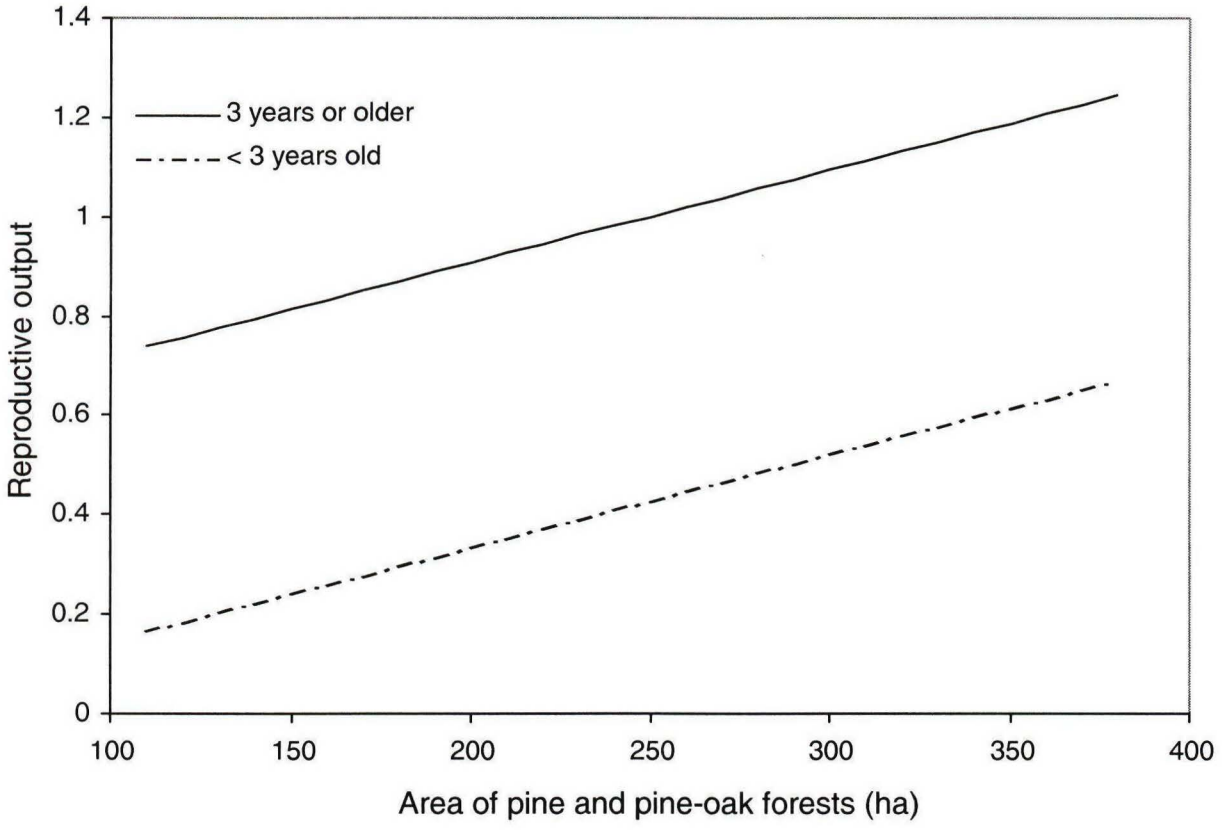

Reproductive output (R)
3
2.5
2
1.5
1
0.5
0
-2.50
-1.50
-0.50
0.50
1.50
2.50
Moisture index

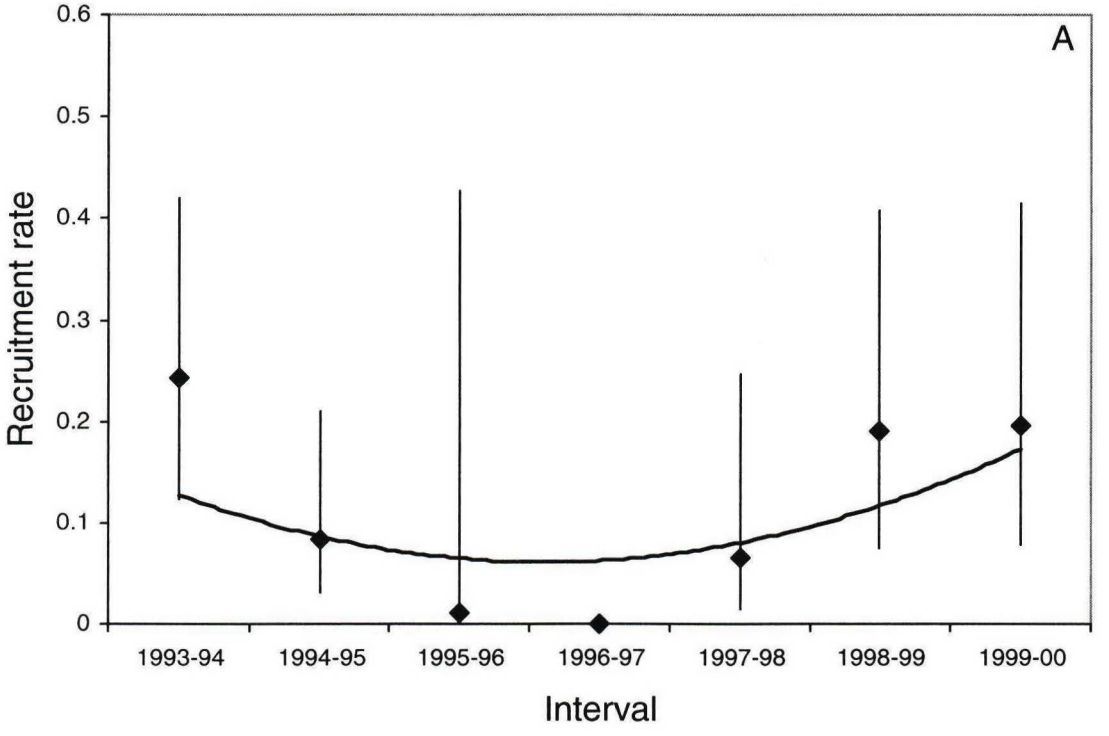

A
Recruitment rate
0.6
0.5
0.4
0.3
0.2
0.1
0
1993-94
1994-95
1995-96
1996-97
1997-98
1998-99
1999-00
Interval

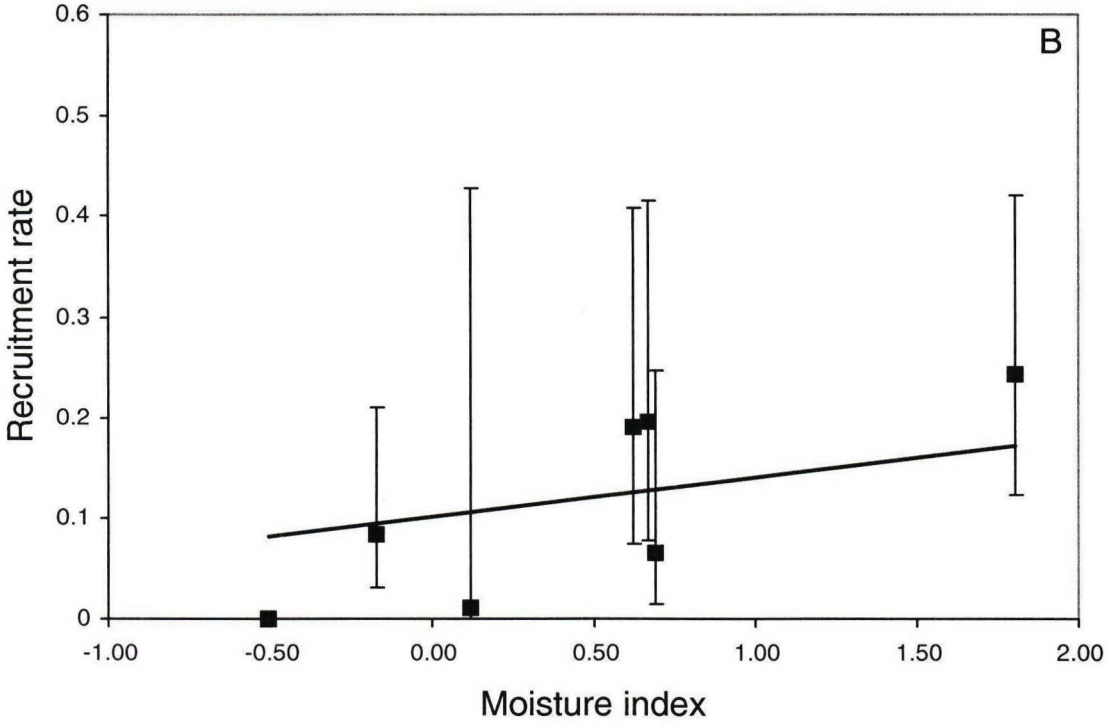

B
Recruitment rate
0.6
0.5
0.4
0.3
0.2
0.1
0
-2.00
-1.50
-1.00
-0.50
0.00
0.50
1.00
1.50
Moisture index


A
1.2
1
0.8
0.6
0.4
0.2
0
Proportion of 1993 population
1993
1994
1995
1996
1997
1998
1999
2000
Year

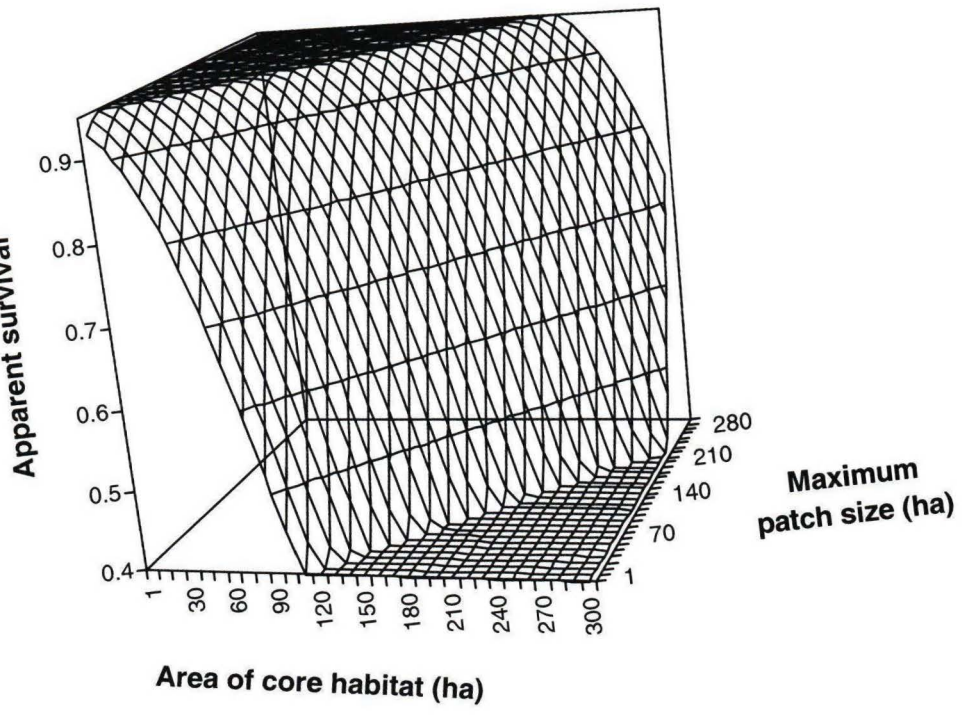

B
1.2
1
0.8
0.6
0.4
0.2
0
Proportion of 1993 population
1993
1994
1995
1996
1997
1998
1999
2000
Year


1.4
1.2
1
0.8
0.6
0.4
0.2
0
Reproductive output
3 years or older
< 3 years old
100
150
200
250
300
350
400
Area of pine and pine-oak forests (ha)

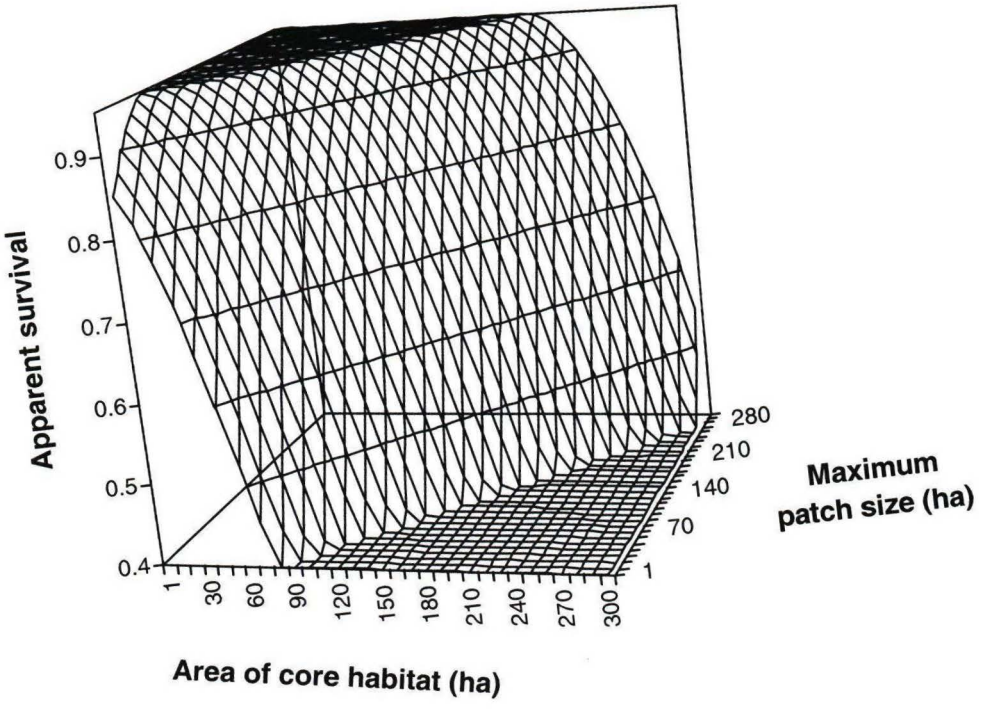

A
Recruitment rate
0.6
0.5
0.4
0.3
0.2
0.1
0
1993-94
1994-95
1995-96
1996-97
1997-98
1998-99
1999-00
Interval

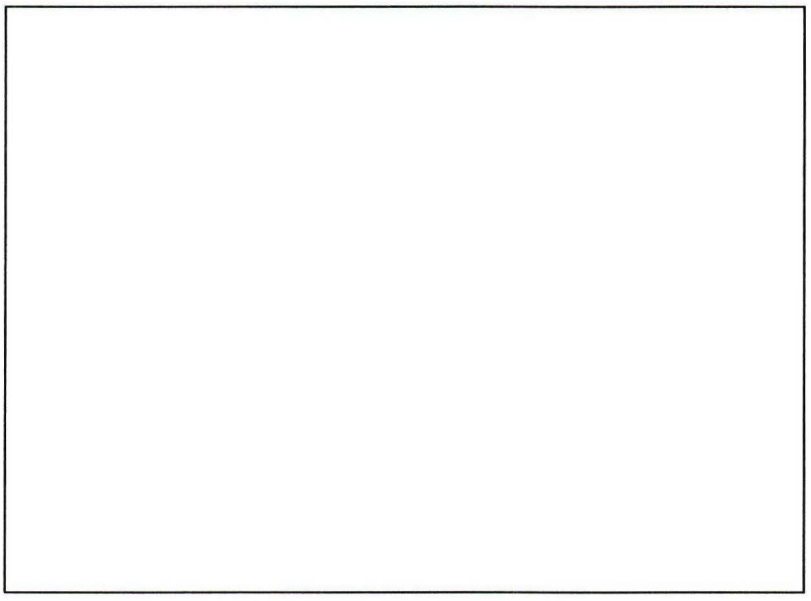

B
Recruitment rate
0.6
0.5
0.4
0.3
0.2
0.1
0
-1.00
-0.50
0.00
0.50
1.00
1.50
2.00
Moisture index

A


Apparent survival
0.9
0.8
0.7
0.6
0.5
0.4
1
30
60
90
120
150
180
210
240
270
300
Area of core habitat (ha)
280
210
140
70
1
Maximum patch size (ha)

B


Apparent survival
0.9
0.8
0.7
0.6
0.5
0.4
1
30
60
90
120
150
180
210
240
270
300
Area of core habitat (ha)
280
210
140
70
1
Maximum patch size (ha)



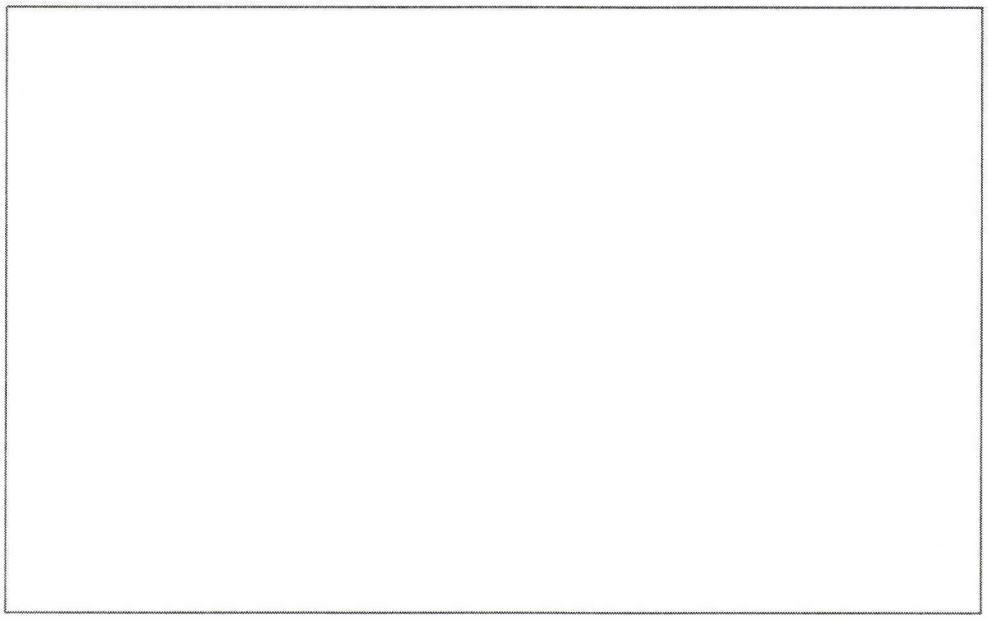


Table 1. *A priori* models used to hypothesize effects of ambient temperature and precipitation (rain and snow) on Mexican spotted owl survival, reproduction, and recruitment. Model parameters are indicated by the following codes : P_Y = annual precipitation, P_W = winter precipitation, P_M = monsoon precipitation, P_E = early nesting season precipitation, P_L = late nesting season precipitation, P_N = total nesting season precipitation, T_W = winter minimum temperatures, T_E = early nesting season minimum temperatures, T_L = late nesting season minimum temperatures, ZNDX = Palmer Z Index for moisture conditions (higher values indicate wetter conditions). Parameters followed by (′) indicate values taken from previous year.

Hypothesis	Model	Model structure	Expected result
Apparent survival (ϕ)			
S1. Positive effect of annual precipitation during the year prior to survival interval.	$\phi(P_Y)$	$\beta_0 + \beta_1(P_Y)$	$\beta_1 > 0$
S2. Positive effect of annual precipitation for t-1 year prior to survival interval.	$\phi(P_{Y'})$	$\beta_0 + \beta_1(P_{Y'})$	$\beta_1 > 0$
S3. Positive threshold effect of annual precipitation during the year prior to survival interval.	$\phi(\ln P_Y)$	$\beta_0 + \beta_1(\ln P_Y)$	$\beta_1 > 0$

S4. Positive threshold effect of annual precipitation for t-1 year prior to survival interval.	ϕ (ln $P_{Y'}$)	$\beta_0 + \beta_1$ (ln $P_{Y'}$)	$\beta_1 > 0$
S5. Negative effect of winter precipitation during survival interval.	ϕ (P_W)	$\beta_0 + \beta_1(P_W)$	$\beta_1 < 0$
S6. Positive effect of winter precipitation 1 year prior to survival interval.	ϕ ($P_{W'}$)	$\beta_0 + \beta_1(P_{W'})$	$\beta_1 > 0$
S7. Positive threshold effect of winter precipitation 1 year prior to survival interval.	ϕ (ln $P_{W'}$)	$\beta_0 + \beta_1$(ln $P_{W'}$)	$\beta_1 > 0$
S8. Interaction effect between winter precipitation and temperature during the winter prior survival interval.	ϕ (P_W*T_W)	$\beta_0 + \beta_1(P_W) + \beta_2(T_W$) + $\beta_3(P_W$*$T_W)$	$\beta_1 > 0, \beta_2 > 0$ $\beta_3 > 0$
S9. Positive effect of monsoon precipitation prior to survival interval.	ϕ (P_M)	$\beta_0 + \beta_1(P_M)$	$\beta_1 > 0$
S10. Positive effects of precipitation during the monsoon prior to and winter during survival interval.	ϕ ($P_M + P_W$)	$\beta_0 + \beta_1(P_M) + \beta_2(P_W)$	$\beta_1 > 0, \beta_2 > 0$
S11. Positive effect of high spring and summer moisture index prior to survival interval.	ϕ (ZNDX)	$\beta_0 + \beta_1$(ZNDX)	$\beta_1 > 0$

Reproductive output (R)

R1. Positive effect of annual precipitation 1 year prior to reproduction.	R (P_Y)	$\beta_0 + \beta_1(P_Y)$	$\beta_1 > 0$
R2. Positive threshold effect of annual precipitation 1 year prior to reproduction.	R ($\ln P_Y$)	$\beta_0 + \beta_1(\ln P_Y)$	$\beta_1 > 0$
R3. Positive effect of winter precipitation prior to reproduction.	R (P_W)	$\beta_0 + \beta_1(P_W)$	$\beta_1 > 0$
R4. Positive effect of monsoon precipitation from previous year.	R (P_M)	$\beta_0 + \beta_1(P_M)$	$\beta_1 > 0$
R5. Positive threshold effect of monsoon precipitation from previous year.	R ($\ln P_M$)	$\beta_0 + \beta_1(\ln P_M)$	$\beta_1 > 0$
R6. Positive effects of precipitation during monsoon and winter periods prior to reproduction.	R ($P_M + P_W$)	$\beta_0 + \beta_1(P_M) + \beta_2(P_W)$	$\beta_1 > 0, \beta_2 > 0$
R7. Positive effect of high spring and summer moisture index during previous year.	R (ZNDX)	$\beta_0 + \beta_1$(ZNDX)	$\beta_1 > 0$
R8. Negative effect of high precipitation in early nesting period.	R (P_E)	$\beta_0 + \beta_1(P_E)$	$\beta_1 < 0$
R9. Negative effect of high precipitation in late nesting period.	R (P_L)	$\beta_0 + \beta_1(P_L)$	$\beta_1 < 0$
R10. Negative effect of high precipitation during nesting period.	R (P_N)	$\beta_0 + \beta_1(P_N)$	$\beta_1 < 0$
R11. Negative effects of a cold, wet nesting period.	R ($P_E + T_E$)	$\beta_0 + \beta_1(P_E) + \beta_2(T_E)$	$\beta_1 < 0, \beta_2 > 0$

R12. Interaction effect between precipitation and temperature during early nesting season.	R (P_E*T_E)	$\beta_0 + \beta_1(P_E) + \beta_2(T_E) + \beta_3(P_E*T_E)$	$\beta_1 < 0, \beta_2 > 0$ $\beta_3 < 0$
R13. Positive effects of high precipitation in monsoon and winter and warm temps in early and late nesting period.	R ($P_M + P_W + T_E + T_L$)	$\beta_0 + \beta_1(P_M) + \beta_2(P_W) + \beta_3(T_E) + \beta_4(T_L)$	$\beta_1 > 0, \beta_2 > 0$ $\beta_3 > 0, \beta_4 > 0$

Recruitment (*f*)

F1. Positive effect of annual precipitation during the year prior to recruitment interval.	$f(P_Y)$	$\beta_0 + \beta_1(P_Y)$	$\beta_1 > 0$
F2. Negative effect of winter precipitation during recruitment interval.	$f(P_W)$	$\beta_0 + \beta_1(P_W)$	$\beta_1 < 0$
F3. Positive effect of monsoon precipitation prior to recruitment interval.	$f(P_M)$	$\beta_0 + \beta_1(P_M)$	$\beta_1 > 0$
F4. Positive effects of precipitation during the monsoon prior to and winter during recruitment interval.	$f(P_M + P_W)$	$\beta_0 + \beta_1(P_M) + \beta_2(P_W)$	$\beta_1 > 0, \beta_2 > 0$
F5. Negative effects of winter precipitation and cold temperatures during recruitment interval.	$f(P_W + T_W)$	$\beta_0 + \beta_1(P_W) + \beta_2(T_W)$	$\beta_1 < 0, \beta_2 > 0$
F6. Negative effects of winter and early nesting period precipitation during recruitment interval.	$f(P_W + P_E)$	$\beta_0 + \beta_1(P_W) + \beta_2(P_E)$	$\beta_1 < 0, \beta_2 < 0$

F7. Positive effect of high spring and summer moisture index prior to recruitment interval.	f(ZNDX)	$\beta_0 + \beta_1$(ZNDX)	$\beta_1 > 0$

Table 2. *A priori* models used to hypothesize effects of habitat components on Mexican spotted owl survival and reproduction. Model parameters are indicated by the following codes: MATFOR = mature forest, MCFOR = mixed conifer forest, MATMCFOR = mature mixed conifer forest, PPOFOR = pine and pine oak forest, YNGFOR = young forest, DOM = dominance (equal area of all forest types), SOEDG = length of forest edge between spotted owl habitat and other vegetation types, SOMP = maximum patch size of spotted owl habitat, SOCOR = total core area of spotted owl habitat, OTHER = amount other habitat.

Hypothesis	Model	Model structure	Expected result
Apparent survival (ϕ)			
S1. Positive effect of more mature forest.	ϕ (MATFOR)	$\beta_0 + \beta_1$(MATFOR)	$\beta_1 > 0$
S2. Positive effect of more mature mixed-conifer forest.	ϕ (MATMCFOR)	$\beta_0 + \beta_1$ (MATMCFOR)	$\beta_1 > 0$
S3. Negative effect of more young forest.	ϕ (YNGFOR)	$\beta_0 + \beta_1$(YNGFOR)	$\beta_1 < 0$
S4. Negative effect of more mixed conifer forest of all age classes.	ϕ (MCFOR)	$\beta_0 + \beta_1$(MCFOR)	$\beta_1 < 0$
S5. Positive effect of more pine and pine-oak forests.	ϕ (PPOFOR)	$\beta_0 + \beta_1$(PPOFOR)	$\beta_1 > 0$
S6. Positive effect of more forest types present.	ϕ (DOM)	$\beta_0 + \beta_1$(DOM)	$\beta_1 > 0$

S7. Positive effect of total amount of primary habitat core areas.	ϕ (SOCOR)	$\beta_0 + \beta_1$(SOCOR)	$\beta_1 > 0$
S8. Positive effect of primary habitat maximum patch size.	ϕ (SOMP)	$\beta_0 + \beta_1$(SOMP)	$\beta_1 > 0$
S9. Positive effect of edge between primary habitats (mature, closed-canopy forest) and other habitats.	ϕ (SOEDG)	$\beta_0 + \beta_1$(SOEDG)	$\beta_1 > 0$
S10. Combined effects of primary habitat total core area, primary habitat maximum patch size, and edge habitat between primary and other habitats (models 7-9 above).	ϕ (SOCOR + SOMP + SOEDG)	$\beta_0 + \beta_1$(SOCOR) + β_2(SOMP) + β_3 (SOEDG)	$\beta_1 > 0$, $\beta_2 > 0$, $\beta_3 > 0$

Reproductive Output (R)

R1. Positive effect of more mature forest.	R (MATFOR)	$\beta_0 + \beta_1$(MATFOR)	$\beta_1 > 0$
R2. Positive effect of more mature mixed-conifer.	R (MATMCFOR)	$\beta_0 + \beta_1$ (MATMCFOR)	$\beta_1 > 0$
R3. Negative effect of more mixed conifer forest of all age classes.	R (MCFOR)	$\beta_0 + \beta_1$(MCFOR)	$\beta_1 < 0$
R4. Positive effect of more mixed conifer forest of all age classes.	R (MCFOR)	$\beta_0 + \beta_1$(MCFOR)	$\beta_1 > 0$

R5. Positive effect of more pine and pine-oak forests.	R (PPOFOR)	$\beta_0 + \beta_1$(PPOFOR)	$\beta_1 > 0$
R6. Positive effect of more "other" habitat.	R (OTHER)	$\beta_0 + \beta_1$(OTHER)	$\beta_1 > 0$
R7. Positive effect of more forest types present.	R (DOM)	$\beta_0 + \beta_1$(DOM)	$\beta_1 > 0$
R8. Positive effect of total amount of primary habitat core areas.	R (SOCOR)	$\beta_0 + \beta_1$(SOCOR)	$\beta_1 < 0$
R9. Positive effect of primary habitat mean patch size.	R (SOMP)	$\beta_0 + \beta_1$(SOMP)	$\beta_1 > 0$
R10. Positive effect of edge between primary habitats and other habitats.	R (SOEDG)	$\beta_0 + \beta_1$(SOEDG)	$\beta_1 > 0$
R11. Combined effects of primary habitat total core area, primary habitat maximum patch size, and edge habitat between primary and other habitats (models 7-9 above).	R (SOCOR + SOMP + SOEDG)	$\beta_0 + \beta_1$(SOCOR) + β_2(SOMP) + β_3(SOEDG)	$\beta_1 < 0$, $\beta_2 > 0$, $\beta_3 > 0$

Table 3. Habitat covariates used for modeling spatial variation in Mexican spotted owl vital rates on 2 study areas in Arizona and New Mexico. Covariates were estimated for each owl territory within 1.1 km radius circles.

Category		Scaling
Covariate	Description[a]	factor[b]
Cover class		
MatFOR	Mature forest, regardless of species composition	ha/100
MatMCFOR	Mature mixed conifer forest	ha/100
MCFOR	Mixed conifer forest, regardless of age class	ha/100
PPOFOR	Pine and pine-oak forests, regardless of age class	ha/100
YngFOR	Young forests, regardless of species composition	ha/100
OTHER	Other[c] cover classes	ha/100
Landscape metric		
DOM	Dominance[d]	NA
SOEDG	Edge between spotted owl habitat[e] and all other habitats	km/100
SOMP	Maximum patch size of spotted owl habitat	ha/100
SOCOR	Sum of spotted owl habitat core areas	ha/100

[a] Arizona: mature forest consisted of ≥6.89 m^2/ha basal area of live trees ≥45.7 cm dbh; young forest consisted of <6.89 m^2/ha basal area of live trees ≥45.7 cm dbh. New Mexico: mature forest consisted of >4.54 m^2/ha basal area of live trees ≥50 cm dbh; young forest consisted of <4.54 m^2/ha basal area of live trees ≥50 cm dbh.

[b] Transformation used to facilitate numerical convergence in analyses.

[c] Other cover classes defined as those in which we did not locate a spotted owl nest tree or roost tree during the study. For Arizona, other cover classes included mature, open canopy pine forest, piñon-juniper woodland, and grassland. For New Mexico, other cover classes included aspen stands, piñon-juniper woodland, and grassland.

[d] Dominance = 1 - (SWDI / ln[s]), where SWDI was the Shannon-Wiener diversity index and ln(s) was the natural log of s, the maximum number of cover classes present on each study area (*sensu* Meyer et al. 1998).

[e] Spotted owl habitat defined as any cover class in which we located a spotted owl nest or roost during the study.

Table 4. The 95% confidence sets of *a priori* hypothesized models examining the effects of age, sex, temporal trends, and climate covariates on apparent survival (ϕ), reproductive output (R), and recruitment (f) of Mexican spotted owls in central Arizona, 1991-2001.

Model[a]	K[b]	AIC_c	ΔAIC_c[c]	w[d]
Apparent survival (all models include p_{t+t^2})				
ϕ_t	13	507.17	0.00	0.738
ϕ_{s+t}	14	509.28	2.11	0.256
Reproductive output				
$R_{female\ a2}$	5	668.0	0.0	0.846
$R_{male\ a2}$	5	672.9	4.9	0.073
R_{ZNDX}	5	675.2	7.2	0.023
R_{PE+TE}	6	676.0	8.0	0.016
Recruitment (all models include ϕ_t, p_{t+t^2})				

f_{t+t^2}	15	1108.54	0.00	0.390
f_t	22	1108.74	0.20	0.353
f_{s+t+t^2}	16	1110.63	2.09	0.137
f_{s+t}	22	1110.90	2.36	0.120

[a] Each section of the table contains the 95% confidence set of models based on AIC_c weights (i.e., the sum of the AIC_c weights in each section is 0.95). The analysis included additional models which are not presented here because they are not likely to explain the data well.

[b] Number of parameters.

[c] Difference in AIC_c value between each model and the "best" model.

[d] AIC_c weight.

Table 5. Components of temporal variation for apparent survival (ϕ), reproductive output (R), and recruitment (f) of Mexican spotted owl populations in Arizona and New Mexico, 1991-2001 (95% confidence limits in parentheses).

Study area	Apparent	Reproductive	Recruitment

Parameter	survival (ϕ)	output (R)	(f)
Arizona			
	0.8592	0.9291	0.1450
ar()[a]	0.0017	0.0352	0.0017
ar(|)[b]	0.0003	0.0045	0.0005
$^2_{temporal}$	0.0129	0.3371	0.0081
	(0.0046, 0.0547)	(0.1536, 1.2424)	(0.0013, 0.0598)
CV()	0.1324	0.6249	0.6217
$^2_{climate}$[c]	0.0067	0.1408	0.0026
$^2_{residual}$	0.0062	0.1963	0.0055
New Mexico			
	0.8561	0.7021	0.0887
ar()	0.0005	0.0394	0.0012
ar(|)	0.0003	0.0050	0.0003
$^2_{temporal}$	0.0016	0.3781	0.0061
	(0, 0.0148)	(0.1756, 1.3237)	(0.0011, 0.0420)
CV()	0.0468	0.8758	0.8777

$^2_{climate}$	0	0.0447	0.0051
$^2_{residual}$	0.0016	0.3334	0.0009

[a] Mean annual variance = $(SE)^2$.

[b] Sampling variation. The percent of mean annual variance due to sampling variation can be calculated as ar(|) / ar() * 100.

[c] The percent of temporal process variation explained by climate can be calculated as $^2_{climate}$ / $^2_{temporal}$ * 100.

Table 6. Results of mixed model analyses used to predict 2002 reproductive output (R) of female Mexican spotted owls in Arizona and New Mexico. We weighted predicted reproductive output estimates according to AIC_c weights, and calculated a single average predictive value.

Study Area					Reproductive output (R)
Model[a]	AIC_c	ΔAIC_c[b]	w[c]	Predicted[d]	Weighted[e]
Arizona					
R_{ZNDX}	675.2	0.00	0.449	0.88	0.40
R_{PE+TE}	676.0	0.80	0.301	1.43	0.43
R_{PY}		679.2	4.00	0.061 0.99	
					0.06
$R_{Pln\ Y}$	679.7	4.50	0.047	1.00	0.05
R_{PE}	680.3	5.10	0.035	1.06	0.04
R_{PL}	680.5	5.30	0.032	0.76	0.02
$R_{Pln\ M}$	680.8	5.60	0.027	0.99	0.03

R_{PW}	681.0	5.80	0.025	0.85	0.02
R_{PM}		681.1	5.90	0.023 0.97	
					0.02
R(weighted average)					**1.06**

New Mexico

$R_{Pln\ Y}$	479.6	0.00	0.174	0.83	0.14
R_{ZNDX}	479.7	0.10	0.165	0.92	0.15
R_{PY}		480.0	0.40	0.142 0.78	
0.11					
R_{PL}	480.5	0.90	0.111	0.55	0.06
R_{PW}	480.5	0.90	0.111	0.48	0.05
$R_{a2'+PN}$	481.3	1.70	0.074	0.57	0.04
$R_{Pln\ M}$	481.7	2.10	0.061	0.67	0.04
R_{PM}		481.7	2.10	0.061 0.66	
0.04					
R_{PE}	481.9	2.30	0.055	0.73	0.04
R_{PE+TE}	482.3	2.70	0.045	0.37	0.02
$R_{a2'+PM+PW}$		482.6	3.00	0.039 0.48	

0.02

R(average of models) **0.72**

[a] Each section of the table contains the 95% confidence set of climate models from the analysis of data from each study area, 1991-2001. The variable for age structure has been removed from all models because it could not be estimated prior to the 2002 field season.

[b] Difference in AIC_c value between each model and the "best" model.

[c] AIC_c weight.

[d] Calculated using climate data for 2001-2002 and statistical models developed using 1991-2001 reproductive output data.

[e] Calculated by multiplying the predicted value by the AIC_c weight.

Table 7. Model selection results for *a priori* hypothesized models of temporal variation in the rate of population change (λ) of a Mexican spotted owl population in central Arizona, 1993-2000. All models included unconstrained survival and recapture structures (i.e., $\{\phi_t, p_t\}$).

Model	K[a]	AIC_c	ΔAIC_c[b]	w[c]
Quadratic random effects	28.21	1120.74	0.00	0.306
Linear random effects	28.41	1120.98	0.24	0.272
Means random effects	28.40	1121.05	0.31	0.263

[a] Number of parameters.

[b] Difference in AIC_c value between each model and the "best" model.

[c] AIC_c weight.

Table 8. The 95% confidence sets of *a priori* hypothesized models examining the effects habitat covariates on apparent survival (ϕ) and reproductive output (R) of Mexican spotted owls in central Arizona, 1991-2001.

Model[a]	K[b]	AIC_c	ΔAIC_c[c]	w[d]
Apparent survival (all models include p_{t+t^2})				
ϕMATFOR	5	476.90	0.00	0.148
ϕYNGFOR	5	477.02	0.12	0.139
ϕSOEDG	5	477.36	0.46	0.117
ϕMATMCFOR		5	477.37	0.47
0.117				
ϕ.	4	477.86	0.96	0.092
ϕSOCOR	5	477.89	0.99	0.090
ϕSOMP	5	478.14	1.24	0.079
ϕMCFOR	5	478.21	1.31	0.077
ϕPPOFOR	5	478.32	1.42	0.073

ϕ_{DOM}	5	479.55	2.65	0.039
Reproductive output				
$R_{a2+PPOFOR}$		6	664.6	0.0
	0.426			
$R_{a2+MCFOR}$		6	666.3	1.7
	0.182			
$R_{a2+MATMCFOR}$		6	667.7	3.1
	0.091			
R_{a2}	5	668.0	3.4	0.078
$R_{a2+SOEDG}$		6	668.6	4.0
	0.058			
$R_{a2+OTHER}$		6	669.6	5.0
	0.035			
$R_{a2+SOCOR}$		6	669.9	5.3
	0.030			
R_{a2+DOM}	6	669.9	5.3	0.030
$R_{a2+MATFOR}$		6	670.1	5.5
	0.027			

[a] Each section of the table contains the 95% confidence set of models based on AIC_c weights (i.e., the sum of the AIC_c weights in each section is 0.95). The analysis included additional models which are not presented here because they are not likely to explain the data well.

[b] Number of parameters.

[c] Difference in AIC_c value between each model and the "best" model.

[d] AIC_c weight.

Table 9. Components of spatial variation for apparent survival (ϕ) and reproductive output (R) of Mexican spotted owl populations in Arizona and New Mexico, 1991-2001 (95% confidence limits in parentheses).

Study area Parameter	Apparent survival (ϕ)	Reproductive output (R)
Arizona		
	0.6683	0.9242
ar()[a]	0.0019	0.0053
ar(|)[b]	0.0002	0.0049
$^2_{spatial}$	0.0953	0.0202
	(0.0668, 0.1466)	(0, 0.0995)
CV()	0.4620	0.1539
$^2_{habitat}$	0.0080	0.0202
$^2_{residual}$	0.0873	0.0000
New Mexico		

	0.6798	0.6743
ar()[a]	0.0023	0.0048
ar(|)[b]	0.0005	0.0029
$^2_{spatial}$	0.0787	0.0772
	(0.0532, 0.1276)	(0, 0.1629)
CV()	0.4127	0.4120
$^2_{habitat}$	0.0214	0.0034
$^2_{residual}$	0.0573	0.0738

[a] Mean territory variance = $(SE)^2$.

[b] Sampling variation. The percent of mean annual variance due to sampling variation can be calculated as ar(\|) / ar() * 100.

[c] The percent of spatial process variation explained by habitat can be calculated as $^2_{habitat}$ / $^2_{spatial}$ * 100.

Table 10. The 95% confidence sets of *a priori* hypothesized models examining the effects of age, sex, temporal trends, and climate covariates on apparent survival (ϕ), reproductive output (R), and recruitment (*f*) of Mexican spotted owls in west-central New Mexico, 1991-2001.

Model[a]	K[b]	AIC_c	ΔAIC_c[c]	w[d]
Apparent survival (all models include p_t)				
ϕ_{a2}	12	597.61	0.00	0.475
$\phi_{.}$	11	601.83	4.22	0.058
ϕ_{PM}	12	601.84	4.23	0.057
$\phi_{Pln\ W'}$	12	602.02	4.41	0.052
$\phi_{PW'}$	12	602.09	4.49	0.050
$\phi_{Pln\ Y'}$	12	602.30	4.69	0.046
$\phi_{Pln\ Y}$	12	602.72	5.11	0.037
$\phi_{PY'}$	12	602.74	5.13	0.036
ϕ_{PY}	12	603.08	5.47	0.031

ϕ_{PM+PW}	13	603.34	5.73	0.027
ϕ_{ZNDX}	12	603.37	5.76	0.027
ϕ_{lt}	12	603.86	6.25	0.021
ϕ_{PW}	12	603.89	6.28	0.020
ϕ_{t+t^2}	13	603.94	6.33	0.020

Reproductive output

R_{a2}	5	469.0	0.0	0.913
$R_{Pln\ Y}$	5	478.1	9.1	0.010
R_{ZNDX}	5	478.2	9.2	0.009
R.	4	478.4	9.4	0.008
R_{lt}	5	478.5	9.5	0.008
R_{PY}	5	478.5	9.5	0.008

Recruitment (all models include ϕ_{PM}, p_t)

f_{t+t^2}	15	1042.02	0.00	0.352
f_{s+t+t^2}	16	1042.19	0.17	0.322
f_t	22	1043.60	1.58	0.160

f_{s+t}	23	1043.90	1.88	0.137

[a] Each section of the table contains the 95% confidence set of models based on AIC_c weights (i.e., the sum of the AIC_c weights in each section is 0.95). The analysis included additional models which are not presented here because they are not likely to explain the data well.

[b] Number of parameters.

[c] Difference in AIC_c value between each model and the "best" model.

[d] AIC_c weight.

Table 11. The 95% confidence sets of *a priori* hypothesized models examining the effects habitat covariates on apparent survival (ϕ) and reproductive output (R) of Mexican spotted owls in west-central New Mexico, 1991-2001.

Model[a]	K[b]	AIC_c	ΔAIC_c[c]	w[d]
Apparent survival (all models include p_{lt})				
ϕ_{a2}+SOEDG+SOMP+SOCOR	7	459.44	0.00	0.296
ϕ_{a2}+MATMCFOR	5	461.16	1.72	0.125
ϕ_{a2}	4	461.36	1.92	0.113
ϕ_{a2}+SOCOR	5	462.05	2.61	0.080
ϕ_{a2}+MATFOR	5	462.34	2.90	0.069
ϕ_{a2}+PPOFOR	5	462.76	3.32	0.056
ϕ_{a2}+YNGFOR	5	462.93	3.49	

		0.052			
ϕ_{a2}+SOMP		5	462.98	3.54	0.050
ϕ_{a2}+SOEDG			5	463.29	3.85
	0.043				
ϕ_{a2}+MCFOR			5	463.33	3.89
	0.042				
ϕ_{a2}+DOM		5	463.41	3.97	0.041
Reproductive output					
R_{a2}		5	469.0	0.0	0.166
R_{a2}+OTHER			6	469.6	0.6
		0.123			
R_{a2}+SOMP		6	469.7	0.7	0.117
R_{a2}+MATFOR			6	470.0	1.0
		0.101			
R_{a2}+SOCOR			6	470.1	1.1
		0.096			
R_{a2}+MATMCFOR			6	470.5	1.5
		0.079			

$R_{a2+SOEDG}$		6	470.5	1.5
		0.079		
$R_{a2+PPOFOR}$		6	470.6	1.6
	0.075			
R_{a2+DOM}	6	470.6	1.6	0.075
$R_{a2+MCFOR}$		6	470.8	1.8
	0.068			

[a] Each section of the table contains the 95% confidence set of models based on AIC_c weights (i.e., the sum of the AIC_c weights in each section is 0.95). The analysis included additional models which are not presented here because they are not likely to explain the data well.

[b] Number of parameters.

[c] Difference in AIC_c value between each model and the "best" model.

[d] AIC_c weight.

[1]Present Address: 268 West Hills Drive, Hattiesburg, Mississippi, 39402; email: chrismay@merlin.ebicom.net

[2]Present Address: Arizona Game and Fish Department, 3500 S. Lake Mary Rd., Flagstaff, Arizona 86001